

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

International Journal of Psychophysiology

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

Emotional scenes and facial expressions elicit different psychophysiological responses

Georg W. Alpers^{a,b,d,*}, Dirk Adolph^{b,c}, Paul Pauli^b

^a School of Social Sciences, Department of Psychology, Chair of Clinical and Biological Psychology, Germany

^b University of Würzburg, Department of Psychology, Germany

^c University of Bochum, Department of Psychology, Germany

^d Otto-Selz-Institute, University of Mannheim, Germany

ARTICLE INFO

Article history:

Received 15 June 2010

Received in revised form 29 December 2010

Accepted 19 January 2011

Available online 26 January 2011

Keywords:

Affect modulated startle

Emotional facial expressions

Emotional scenes

Autonomic responses

Valence and arousal ratings

ABSTRACT

We examined if emotional faces elicit physiological responses similar to pictures of emotional scenes. Forty one students viewed emotional scenes (negative, neutral, and positive) and emotional faces (angry, neutral, and happy). Heart rate, orbicularis oculi and electrodermal activity were measured continuously, and the startle reflex was elicited. Although the patterns of valence and arousal ratings were comparable, physiological response patterns differed. For scenes we replicated the valence-specific modulation of the startle response, heart rate deceleration, and the arousal-related modulation of the electrodermal response. In contrast, for faces we found valence-specific modulation only for the electrodermal response, but the startle and heart rate deceleration were modulated by arousal. Although arousal differences may account for some differences in physiological responding this shows that not all emotional material that is decoded similarly leads to the same psychophysiological output.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Emotions are thought to be part of two basic motivational systems (Lang, 1995) where the appetitive system activates approach behavior when consummation, procreation or nurturance is the goal and the defensive system activates defense behavior in order to protect the organism from threat. These two systems modulate reflex responses that are compatible or incompatible with the required behavior. Within this framework, emotional reactions to external cues are modulated by two dimensionally organized stimulus features: valence and arousal. Judgments of valence, i.e., pleasure or displeasure, relate to the active motivational system and judgments of arousal relate to the intensity of motivational activation (Bradley et al., 2001). Pictures of emotional scenes (Lang, 1995) and emotional facial expressions (Russell and Bullock, 1985) can be described by ratings on these two dimensions. Evidence for this motivational theory of emotion comes from an impressive number of studies using the picture viewing paradigm to elicit approach and avoidance motivation (Bradley et al., 2001; Lang et al., 1997).

1.1. Emotional scenes

To document activation of the defensive or appetitive system, several physiological variables, including the affective modulation of the startle reflex are typically used. It has been well demonstrated that the amplitude of the eyeblink startle reflex elicited by a loud noise varies with emotional valence of the background stimulus viewed simultaneously. The response is potentiated when viewing slides with negative content, and reduced when viewing positive pictures (Vrana et al., 1988). In addition, measures of autonomic activity covary with the level of arousal or with the valence of the presented stimulus (Bradley et al., 2001). The typical pattern of defensive motivation is an initial heart rate deceleration which indicates orientation towards a meaningful stimulus (Graham, 1997; Graham and Clifton, 1966).

The electrodermal response seems to be an unspecific measure of arousal. A significant rise of the skin conductance level can be found for both positive and negative stimuli when compared to neutral ones (e.g., Azevedo et al., 2005; Bradley et al., 2001, 2005).

Other valence-specific responses can be measured with the facial EMG: the corrugator supercilii muscle, which causes frowning, is more strongly activated when watching negative scenes and the zygomatic major (Lang et al., 1993), as well as the orbicularis oculi muscle (as a part of the so called Duchenne smile, Wolf et al., 2005) are engaged while watching positive slides.

In the central nervous system, the emotional responses observed in the picture viewing paradigm are probably orchestrated by the amygdala (LeDoux, 2000; Whalen, 1998). Several studies have shown

* Corresponding author at: University of Mannheim, Chair of Biological and Clinical Psychology, School of Social Sciences, 68131 Mannheim, Germany. Tel.: +49 621 181 2106; fax: +49 621 181 2107.

E-mail address: alpers@uni-mannheim.de (G.W. Alpers).

that significant amygdala activations can be observed when the responses to emotional scenes and neutral scenes are contrasted (e.g., Hariri et al., 2002; Lee et al., 2004; Müller et al., 2003) (for a review see Phan et al., 2004).

1.2. Emotional facial expressions

Because the picture viewing paradigm has been so prolifically used with complex emotional scenes, it is surprising that there are so little published data on physiological reactions to emotional facial expressions. While emotional faces have been shown to be processed similar to emotional scenes in many ways, e.g., they both predominate perceptually in binocular rivalry (Alpers and Gerdes, 2007; Alpers and Pauli, 2006), direct comparisons of physiological or behavioral output are rare.

Emotional facial expressions should be particularly well suited to elicit evolutionarily grounded motivational responses. While the meaning of most scenes can only be deciphered when several elements are integrated, faces are processed holistically (Farah et al., 1998). Moreover, facial expressions are generally thought to be biologically rooted (Dimberg et al., 2000), comparable across cultures (Ekman et al., 1969), and they clearly evoke emotional responses in everyday life (Dimberg, 1982). Similar to pictures of emotional scenes (e.g., Alpers, 2008), emotional expressions have been shown to capture attention in visual search tasks (Hansen and Hansen, 1988; Öhman et al., 2001) and in the dot-probe deployment paradigm (Bradley et al., 1997; Mogg and Bradley, 2002). Within the framework of the somatic marker hypothesis it has been argued that the perception of an emotional expression involves the simulation of the emotional state within the relevant cortical circuitry of the observer (Adolphs, 2002). Several brain imaging studies have shown that both positive and negative emotional facial expressions strongly activate the amygdala (for a review see Zald, 2003) and this activation can be found even when the faces are not consciously visible due to masking (Whalen et al., 1998, 2004).

As in response to scenes, the facial EMG activity response corresponds with the valence of an emotional expression: the corrugator supercilii muscle is more strongly activated when negative facial expressions are attended to, and the zygomatic major muscle is more strongly activated when positive facial expressions are observed (Dimberg, 1982; Dimberg and Petterson, 2000; Vrana and Gross, 2004). More specifically, the so called Duchenne smile has been found as a response to positive, rather than to negative facial expressions (Hess et al., 1998).

Contrary to the results including facial EMG, studies on physiological responses to faces are rare and revealed less consistent results as for emotional scenes. Concerning the electrodermal response some studies found comparable reactions to angry and happy facial expressions (Dimberg, 1982; Merckelbach et al., 1989) or even stronger electrodermal responses to happy expressions than to angry ones (Vrana and Gross, 2004). Concerning heart rate, at least two studies found the expected heart rate deceleration to angry facial expressions, but heart rate acceleration to happy expressions (Johnsen et al., 1995; Vrana and Gross, 2004). However, in Vrana and Gross (2004) study deceleration was also observed for neutral faces, and an earlier study did not find any differences in deceleration between angry and happy expressions (Dimberg, 1982).

Published data on the startle response to emotional facial expressions is also rather limited and shows contradictory results. There is one study demonstrating that the affective modulation of the startle reflex to angry and happy expressions can be found in 5 month old infants (Balaban, 1995), while a recent study did not find affect modulated startle responses to neutral and angry facial expressions in four to eight year old children (Waters et al., 2008). In adults, one study with pictures of negative infant emotional faces (crying babies) did not find the expected startle modulation (Spangler et al., 2001). Another study found a startle potentiation to threatening adult facial expressions (i.e., fearful and angry expressions, Anokhin and Golosheykin, 2009). Finally,

a study by Hess et al. (2007) reported startle reflex potentiation to angry emotional faces but the expected potentiation was only found when the actors were males, whereas results by Springer et al. (2007) suggest that startle amplitudes may be potentiated while viewing angry facial expression regardless of the sex of the expresser. To our knowledge, no study to date found the expected inhibition of the startle reflex to appetitive (e.g. happy) emotional facial expressions.

However, few studies have directly compared the responses to faces and to scenes. Two recent experiments (Britton et al., 2006; Hariri et al., 2002) demonstrated within the same experimental paradigm that emotional scenes and faces activate similar brain structures, including those directly engaged in emotion processing like the amygdala. However, faces were superior in eliciting stronger activations in the amygdala (Hariri et al., 2002) or activations in more extended regions beyond it (Britton et al., 2006). In spite of the similarities in brain activations, it is not resolved, whether this reflects the decoding of emotional cues or whether it also corresponds with comparable physiological output. That physiological responses to emotional facial expressions emotional and scenes may differ has been demonstrated by one of the imaging studies mentioned above: electrodermal responding to negative facial expressions was more pronounced than that to comparable scenes (Hariri et al., 2002). However, other responses, such as the startle modulation were not examined in that study.

1.3. Aims

The aim of the present experiment was to directly compare the psychophysiological effects of emotional facial expressions and emotional scenes in order to clarify whether emotional facial expressions and emotional scenes induce comparable appetitive and defensive motivation. On the one hand, we assumed that comparable or even greater amygdala activity observed in response to emotional facial expressions should lead to comparable activation of the defensive and appetitive motivational system, and hence to comparable patterns of physiological responses. On the other hand, the evidence we accumulated from different studies suggest that despite comparable activation patterns in significant emotion related brain areas, the physiological output to emotional facial expressions, but not for emotional scenes, is inconsistent. The strongest argument as to why differences in physiological output to scenes and faces should be expected is based on the finding that the modulation of physiological output is dependent on the level of arousal a stimulus induces. For example, the emotional modulation of the startle response can typically only be observed in pictures that elicit relatively high levels of arousal (Cuthbert et al., 1996), and the fact that emotional facial expressions often only elicit relatively low levels of arousal (e.g., Alpers and Gerdes, 2007). In order to address this question, we examined the influence of differences in the perceived level of arousal between scenes and facial expressions on the psychophysiological responses measured in an analysis of covariance.

Therefore, we presented a block of happy, neutral, and angry faces and a block of positive, neutral, and negative scenes. To assess the activation of defensive and appetitive motivational systems in response to the scenes and faces, we measured heart rate deceleration and electrodermal responding to picture onset and the modulation of the startle reflex elicited by a loud noise while participants viewed the pictures. In addition to these classic measures we also explored the usefulness of the EMG from the orbicularis oculi muscle (which is typically recorded for the startle response) as a continuous measure of facial expressiveness indexing the Duchenne smile.¹ The EMG is thought to reflect a valence-specific response (Wolf et al., 2005). Also, we collected ratings of picture valence and arousal.

¹ As mentioned above, the so-called Duchenne smile consists of simultaneous activation of the zygomaticus major and the orbicularis oculi muscle. Within the scope of this work we assessed the latter component only.

2. Method

2.1. Participants

Participants were 41 (15 male) undergraduate psychology students, with an age range of 19 to 42 years ($M = 22.4$, $SD = 4.4$). Scores on the German version of the State Trait Anxiety Inventory (STAI; [Laux et al., 1981](#)) and on the German version of the Social Phobia Anxiety Inventory (SPAI; [Fydrich, 2001](#)) were somewhat higher than normative data (STAI: $M = 41.8$, $SD = 10.2$; SPAI: $M = 3.3$, $SD = 0.9$). However, they were well within the range of our previous student samples ([Alpers and Gerdes, 2007](#); [Alpers and Pauli, 2006](#); [Alpers et al., 2005](#)). One participant decided not to participate because of the aversive nature of the startle probe. Two participants had to be excluded because they closed their eyes in response to most negative scenes (this was based on both self-report and the facial EMG). One participant was excluded from ECG analyses due to excessive artifacts in this signal, but his data was used for all other analyses. All participants gave written informed consent. They received course credit for their participation. The study has been performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

2.2. Material

Pictures of scenes were 11 positive, 11 negative, and 11 neutral slides from the International Affective Picture System (IAPS; [Lang et al., 2005](#)), selected to be most similar in arousal ratings for positive and negative pictures.² The IAPS pictures were chosen to represent relatively wide varieties of negative (e.g. attacking animals, human mutilation, and human attack), neutral (e.g. mushrooms, household objects, and buildings) and positive (e.g. babies, erotic couples, and fun sports) picture contents. Pictures of facial expressions were 11 positive (happy), 11 negative (angry), and 11 neutral facial expressions from the NimStim set ([Tottenham et al., 2009](#)).³ All emotions were represented by each actor. Only pictures from female actors were presented because they were reported to evoke stronger emotional responses in previous research ([Wild et al., 2001](#)). Furthermore, in a pilot study arousal ratings were more similar between angry and happy expressions for female than for male actors ([Adolph and Alpers, 2010](#)). Those facial expressions were chosen which achieved the highest arousal ratings in the two relevant categories in the pilot study. The pictures were adjusted using Photoshop™ to closely resemble each other in luminance and color depth. Pictures were shown on a 19 in. monitor placed 1 m in front of the participant, resulting in a visual angle of 27° by 22°. Picture presentation was timed and randomized by Presentation (Neurobehavioral Systems, USA).

2.3. Apparatus

2.3.1. Data recording

All physiological data were recorded with a 16 bit Varioport II system (Becker Meditec, Karlsruhe, Germany) at a sampling rate of 1024 Hz. Orbicularis oculi EMG activity and electrodermal activity

were each recorded with 2 Ag/AgCl mini electrodes (5 mm diameter). For the EMG they were filled with isotonic electrode gel, for EDA with non-hydrating NaCl paste. EMG electrodes were attached under the left eye according to [Fridlund and Cacioppo \(1986\)](#), and the EMG was amplified online. Two EDA electrodes were placed at the thenar and hypothenar of the non-dominant hand and a constant current of 0.5 V was applied. The EKG was recorded with 2 large Ag/AgCl disposable electrodes filled with electrode gel. The electrodes were attached to the right clavicle and the lowest rib on the left within the axillary line. An Ag/AgCl ground electrode was attached to the left clavicle.

2.3.2. Startle stimulus

The acoustic startle stimulus was a 50 ms burst of white noise at 100 dB(A). This stimulus was generated by Presentation® using a standard 24 bit sound card and amplified with a HiFi amplifier (KA 3010 Kenwood). It was presented binaurally over headphones (DT 901, Bayerdynamic).

2.4. Procedure

During the experiment the participants sat in a comfortable chair in a dimly lit room. After completing a socio-demographic questionnaire, the skin was cleansed and the sensors were attached. The participants were then instructed to relax and keep their attention towards the monitor, even during the inter-trial intervals when no pictures were shown. They were shown an example of every picture category, and were informed that some of the pictures might be accompanied by an uncomfortable noise which should be ignored.

Facial expressions and scenes were presented in two counter-balanced blocks of 33 slides each. Within each block the slides were presented in random order. Pictures were presented for 6 s with an inter-trial interval varying randomly between 16 and 24 s. Six acoustic startle probes were administered before the first block to induce habituation. During each experimental block, startle probes were delivered during six pictures of each emotion category and during two inter-trial intervals. Timing varied randomly between the third and fifth second after stimulus onset.

After the first block participants were given a break and asked to fill in the questionnaires. At the very end of the session participants rated valence and arousal for each picture; scenes and faces were presented in counterbalanced order. Participants were asked how they felt (range 1 to 9: 1 = very negative, 5 = neutral, 9 = very positive) and how emotionally aroused they were (range 1 to 9: 1 = not at all aroused, 9 = very aroused) while viewing each picture.

2.5. Data reduction and analyses

All physiological channels were analyzed off-line. They were first filtered with a 50 Hz notch filter. To assess startle eyeblink responses the raw EMG signal was rectified, and frequencies below 20 Hz ([van Boxtel et al., 1998](#)) and above 500 Hz ([Blumenthal et al., 2005](#)) were filtered. The data were then integrated with time constants of 20 ms (for startle latency detection) and 100 ms (for peak amplitude detection). According to [Blumenthal et al. \(2005\)](#) the startle eyeblink reflex was defined as the first maximum increase of EMG activity of the orbicularis oculi in a time interval between 20 and 150 ms after startle probe onset. From this, the mean EMG of the 20 ms baseline directly preceding the onset was subtracted to measure startle amplitude. Startle amplitude values were T-transformed to reduce the impact of outliers. No more than three trials per category and participant had to be excluded from further analyses due to excessive noise in the baseline interval ([Blumenthal et al., 2005](#)) so that we did not have to exclude data from any participant.

For the analysis of SCR, heart rate, as well as for the orbicularis oculi EMG responses data from all 11 trials were included into our analysis. For the orbicularis activity, frequencies below 90 Hz and

² Emotional scenes (IAPS) and faces (NimStim) for trials which were used for analyses of physiological data. IAPS negative: 1120, 1300, 3010, 6230, 6350, and 9040; neutral: 5500, 7010, 7100, 7140, 7500, and 7550; positive: 2070, 1710, 4660, 4680, 7330, and 8190. NimStim negative: 01F_AN_O, 02F_AN_O, 03F_AN_O, 08F_AN_O, 10F_AN_O, and 17F_AN_O; neutral: 02F_NE_C, 03F_NE_C, 08F_NE_C, 09F_NE_C, 17F_NE_C, and 18F_NE_C; positive: 01F_HA_O, 08F_HA_O, 09F_HA_O, 10F_HA_O, 17F_HA_O, and 18F_HA_O.

³ According to an expert rating (Dr. Heiner Ellgring, University of Würzburg) all happy faces represent genuine Duchenne smiles with the action units 6, 12, and 25 engaged ([Ekman and Rosenberg, 1997](#)).

Table 1
Mean (and standard deviations) self-report ratings and physiological responses to negative, neutral, and positive emotional scenes and angry, neutral and happy facial expressions.

	Scenes						Faces					
	Negative		Neutral		Positive		Negative (angry)		Neutral		Positive (happy)	
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Valence Rating	2.31	0.7	5.28	0.4	7.10	0.8	3.12	0.9	4.58	0.5	6.46	0.9
Arousal Rating	6.63	1.3	2.57	1.4	5.5	1.2	4.53	1.7	3.06	1.5	4.44	1.6
Startle Amplitude	51.72	5.1	49.48	4.9	47.42	5.8	51.95	5.1	50.02	5.3	51.49	4.3
Δ HR	-2.50	2.7	-1.06	2.4	-1.14	1.5	-0.94	2.1	-1.63	2.3	-0.97	2.5
Δ SCR	0.019	0.02	0.011	0.02	0.013	0.02	0.012	0.01	0.015	0.02	0.017	0.02
Δ Orbicularis EMG	-0.16	0.75	-0.16	1.04	0.47	0.83	-0.48	1.52	-0.10	0.79	-0.12	0.96

Δ change from baseline.

above 500 Hz were filtered from the orbicularis oculi EMG, and the signal was integrated with a time constant of 20 ms (see Dimberg, 1990). The EMG response was baseline-corrected by subtracting data from a 100 ms baseline preceding the trial in 100 ms steps, and an average for the first three seconds of each trial was calculated.⁴

For the heart rate response, R-spikes were marked in the EKG and inter-beat-intervals were calculated and transformed into beats per minute, in one second bins (see Bradley et al., 2001; Gatchel and Lang, 1974; Hodes et al., 1985). To determine initial heart rate deceleration as the orienting response (Bradley et al., 2001), changed scores were calculated with mean beats per minute for the first three seconds of picture presentation relative to a three second baseline period directly preceding stimulus onset.

The EDA signal was integrated with a time constant of 20 ms. Skin conductance responses (SCR) were defined as the maximum peak of electrodermal activity in a 5 s interval beginning 1 s after stimulus onset and ending with stimulus-offset (according to Boucsein, 1992). These values were baseline-corrected by subtracting the maximum within a 1000 ms period before stimulus onset. These data were then log transformed ($\log[\text{SCR} + 1]$).

To assess valence effects, separate ANOVAs were run for each physiological measure and the rating data, with the within-subject variables picture set (faces and scenes) and emotion (negative, neutral, and positive). Where appropriate, Greenhouse–Geisser corrections of degrees of freedom were calculated and adjusted *p*-values are reported. We followed up on significant main effects and interactions with *t*-tests.

Furthermore, to address possible effects of the order of presentation in our random block design, we ran a second set of ANOVAs with presentation order as a between-subject variable. Because none of these ANOVAs revealed any significant main effects or interactions involving presentation order (all $p > .10$), the effects of the ANOVAs run without this factor are reported.

A separate set of ANCOVAs was run in order to investigate the impact of possible differences in perceived levels of arousal elicited by the scenes and faces. Therefore, difference scores between subjective arousal ratings elicited by the scenes and faces were calculated for every emotion category (i.e., negative IAPS-angry KDEF, neutral IAPS-neutral KDEF, and positive IAPS-happy KDEF). These difference scores were then entered as covariates into ANCOVAs with the within-subject variables picture set (faces and scenes) and emotion (negative, neutral, and positive).

⁴ Because startle probes were delivered after three seconds of picture presentation, the orbicularis oculi EMG was averaged for the first three seconds of picture presentation only. Given the time course of the Duchenne smile, most authors recommend larger time slots, or average activation over the entire course of picture delivery. However, given that the duration of a 'felt smile', even in response to strong positive feelings, are thought to not exceed 4000 ms (Ekman and Friesen, 1982), a time frame of 3000 ms may be able to cover the onset, as well as a major part of the apex of the orbicularis oculi responses to the stimuli.

3. Results

3.1. Self-report ratings

Table 1 shows means and standard deviations for valence and arousal ratings to facial expressions and scenes.

3.1.1. Valence

The ANOVA for valence ratings revealed a significant main effect for emotion, $F(2, 78) = 361.99, p < .001, \eta_p^2 = .90$, a significant main effect for picture set, $F(1, 39) = 5.05, p = .030, \eta_p^2 = .12$, and a significant interaction for picture set by valence, $F(2, 78) = 42.25, p < .001, \eta_p^2 = .52$. Follow-up *t*-tests showed that the emotion main effect followed the expected pattern for scenes and faces: negative scenes were rated more negatively than neutral, $t(39) = 20.50, p < .001$, and positive scenes, $t(39) = 22.86, p < .001$, and neutral scenes more negative than positive scenes, $t(39) = 13.77, p < .001$. Similarly, negative facial expressions were rated more negative than neutral, $t(39) = 10.78, p < .001$, and positive expressions, $t(39) = 13.67, p < .001$, and neutral faces were rated more negative than positive ones, $t(39) = 13.77, p < .001$. For both sets, there was a significant linear contrast (scenes, $F(1, 39) = 522.73, p < .001, \eta_p^2 = .93$; and faces, $F(1, 39) = 187.64, p < .001, \eta_p^2 = .83$). The interaction was due to negative scenes being more negative than negative faces, $t(39) = 6.398, p < .001$, whereas neutral, $t(39) = 7.82, p < .001$, and positive scenes, $t(39) = 3.75, p = .001$, were rated more positive than the corresponding expressions.

3.1.2. Arousal

The ANOVA for arousal ratings revealed a significant main effect for emotion, $F(2, 78) = 138.98, p < .001, \eta_p^2 = .78$, a significant main effect for picture set, $F(1, 39) = 28.43, p < .001, \eta_p^2 = .44$, and a significant interaction, $F(2, 78) = 45.38, p < .001, \eta_p^2 = .54$. Follow-up tests showed that the emotion main effect followed the expected pattern for scenes and faces: Neutral scenes were rated less arousing than negative, $t(39) = 14.93, p < .001$, and positive scenes, $t(39) = 13.10, p < .001$, but positive scenes were rated somewhat less arousing than negative scenes, $t(39) = 6.66, p < .001$. Similarly, neutral facial expressions were rated less arousing than negative, $t(39) = 5.88, p < .001$, and positive expressions, $t(39) = 5.90, p < .001$. Arousal ratings for positive and negative facial expressions did not differ significantly from each other, $t(39) = 0.54, p = .591$. For both sets, there was a significant quadratic trend (scenes, $F(1, 39) = 221.94, p < .001, \eta_p^2 = .85$, and faces, $F(1, 39) = 38.64, p < .001, \eta_p^2 = .50$). The interaction was due to negative scenes being more arousing than negative faces, $t(39) = -9.76, p < .001$, and positive scenes more arousing than positive faces, $t(39) = 4.33, p = .001$, but neutral scenes were less arousing than neutral faces, $t(39) = 2.14, p = .039$.

3.2. Physiological responses

3.2.1. Startle response

Fig. 1 shows mean startle amplitudes (and standard errors of the mean) for scene and face trials; startle responses are clearly modulated by emotional background pictures but the patterns are different for scenes and faces (exact means and standard deviations are listed in Table 1). The ANOVA did not reveal a significant main effect for picture set, $F(1, 38) = 1.49, p = .230, \eta_p^2 = .04$. However, there was a significant main effect for emotion, $F(2, 76) = 10.10, p < .001, \eta_p^2 = .21$, and a significant interaction for picture set by emotion, $F(2, 76) = 7.40, p = .002, \eta_p^2 = .16$. Follow-up *t*-tests showed that the expected emotional modulation was only present in scenes, and not faces. While viewing negative scenes startle responses were potentiated compared to neutral scenes, $t(38) = 5.56, p = .015$, and to positive scenes, $t(38) = 4.90, p < .001$. Furthermore, during neutral scenes startle responses were greater than during positive scenes, $t(38) = 2.53, p = .016$. For scenes there was a significant linear trend, $F(1, 38) = 23.94, p < .001, \eta_p^2 = .39$. In contrast, while viewing negative facial expressions startle responses were significantly potentiated only compared to neutral expressions, $t(38) = 2.28, p = .028$, but not to positive expressions, $t(38) = 0.75, p = .460$. Furthermore, there was a statistical trend for potentiated startle responses during positive expressions compared to neutral expressions, $t(38) = 1.94, p = .060$. This pattern was confirmed by a significant quadratic trend for emotional facial expressions, $F(1, 38) = 5.23, p = .028, \eta_p^2 = .12$. The interaction of set by emotion came about because startle amplitudes while viewing negative and neutral pictures did not significantly differ between scenes and faces (both $p > .10$), but startle amplitudes were greater for positive facial expressions than for positive scenes, $t(38) = 2.79, p = .008$.

3.2.2. Heart rate

Table 1 lists mean heart rate responses (and standard deviations) for scene and face trials; viewing emotional scenes or facial expressions clearly resulted in different patterns of heart rate responses (Fig. 2). In the ANOVA there were no significant main effects for picture set and for emotion (both $p > .10$). However, there was a significant interaction for picture set by emotion, $F(2, 74) = 5.68, p = .005, \eta_p^2 = .13$. Follow-up *t*-tests showed that viewing scenes lead to the expected pattern with greater heart rate deceleration during negative than neutral, $t(37) = 2.42, p = .020$, and positive scenes, $t(37) = 3.03, p = .004$. Although there was no difference between neutral and positive scenes, $t(37) = 0.18, p = .858$, there was a significant linear trend for all emotions in scenes, $F(1, 37) = 9.19, p = .004, \eta_p^2 = .20$. In contrast, viewing facial expressions lead to an unexpected pattern with deceleration in all three conditions. There was no difference between positive and negative

expressions, $t(37) = 0.05, p = .959$, and between negative and neutral expressions, $t(37) = 1.38, p = .177$. The marginally significantly greater heart rate deceleration during neutral than positive expressions, $t(37) = 1.78, p = .083$, corresponds with the marginally significant quadratic trend for facial expressions, $F(1, 37) = 3.14, p = .085, \eta_p^2 = .08$. The interaction of picture set by emotion was further explained by greater heart rate deceleration during negative scenes than negative faces, $t(37) = 3.00, p = .005$, and no difference between positive or neutral scenes and faces (all $p > .10$).

3.2.3. Skin conductance response

Table 1 lists mean skin conductance responses (and standard deviations) for scene and face trials. Viewing emotional scenes or facial expressions clearly resulted in different patterns of skin conductance responses (Fig. 3). In the ANOVA there were no significant main effects for picture set and for emotion (both $p > .10$). However, there was a significant interaction for picture set by emotion, $F(2, 76) = 5.25, p = .008, \eta_p^2 = .10$. Follow-up *t*-tests showed that viewing scenes lead to the expected pattern with greater skin conductance responses to negative than to neutral scenes, $t(38) = 3.03, p = .004$, and marginally significant, compared to positive scenes, $t(38) = 1.90, p = .065$. However, there was no significant difference in the skin conductance response between neutral and positive scenes, $t(38) = 0.74, p = .461$, but there was a quadratic trend for all emotions in scenes, $F(1, 38) = 4.98, p = .032, \eta_p^2 = .12$. In contrast, viewing facial expressions lead to a statistical trend for greater skin conductance responses to positive than negative expressions, $t(38) = 1.90, p = .067$. Responses to neutral faces did not differ from negative, $t(38) = 1.14, p = .260$, or positive facial expressions, $t(38) = 0.88, p = .384$. However, there was a marginally significant linear trend for all emotions in faces, $F(1, 38) = 3.56, p = .067, \eta_p^2 = .09$. The interaction of picture set by emotion was further explained by greater skin conductance responses to negative scenes than to negative faces, $t(38) = 2.25, p = .030$, and no difference between neutral, $t(38) = 1.10, p = .278$, or positive, $t(38) = 1.10, p = .279$, scenes and faces.

3.2.4. Orbicularis activity

Table 1 lists mean responses in the orbicularis oculi facial EMG (and standard deviations) for scene and face trials. In the ANOVA there was a significant main effect for picture set, $F(1, 38) = 5.34, p = .026, \eta_p^2 = .12$, indicating that overall, faces elicited smaller orbicularis oculi responses than scenes. The significant main effect for emotion, $F(2, 76) = 4.69, p = .017, \eta_p^2 = .11$, and the corresponding follow-up tests showed that viewing positive stimuli leads to the expected pattern with more orbicularis activity than viewing neutral, $t(38) = 2.36, p = .023$, and negative stimuli, $t(38) = 2.61, p = .013$,

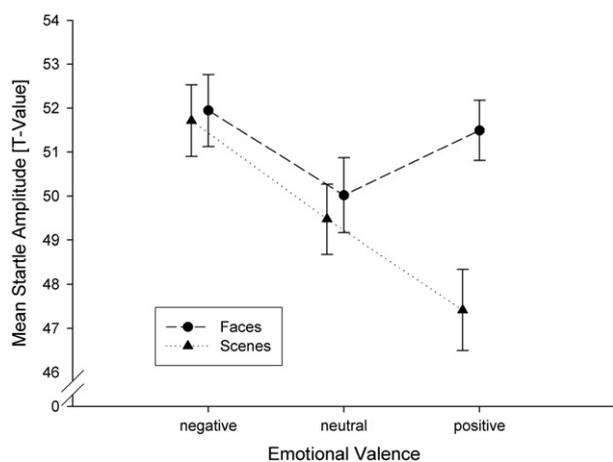


Fig. 1. Means (+/–SEM) of startle amplitudes in response to emotional scenes (triangles) or emotional facial expressions (circles).

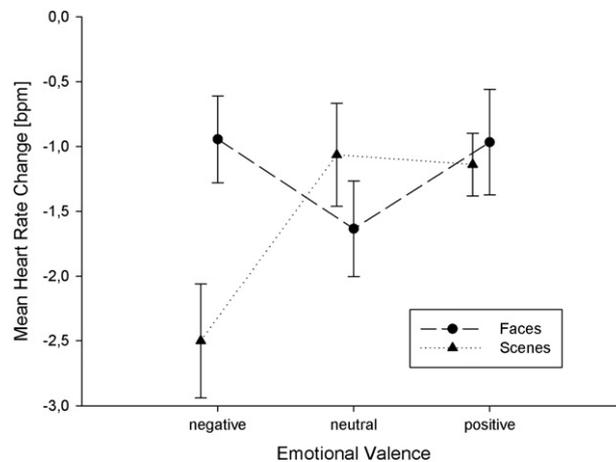


Fig. 2. Means (+/–SEM) of the heart rate response in response to emotional scenes (triangles) or emotional facial expressions (circles).

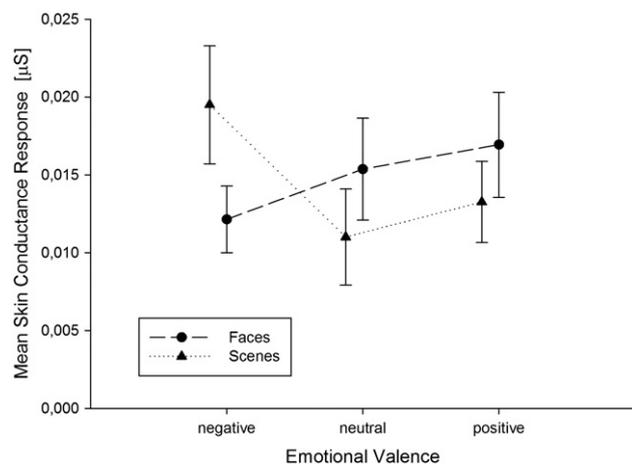


Fig. 3. Means (+/–SEM) of the skin conductance response in response to emotional scenes (triangles) or emotional facial expressions (circles).

but EMG reactions to neutral and negative stimuli did not differ significantly, $t(38) = 1.14$, $p = .262$. There was a linear trend for the three emotions, $F(1, 38) = 6.83$, $p = .013$, $\eta_p^2 = .15$. There was no significant interaction for picture set by emotion ($p > .10$).

3.3. Control for differences in self-report arousal

3.3.1. Startle response

The ANCOVA controlling for differences in arousal ratings revealed a significant main effect for emotion, $F(2, 70) = 5.00$, $p = .009$, $\eta_p^2 = .13$. Viewing negative stimuli lead to elevated startle responses compared to neutral, $t(38) = 3.50$, $p = .001$, and positive stimuli, $t(38) = 4.21$, $p < .001$, which elicited comparable startle responses, $t(38) = 0.50$, $p = .612$. However, there was no main effect for picture set and no interaction for picture set by emotion (both $p > .10$).

3.3.2. Heart rate

Controlling for differences in arousal ratings did not affect the significant interaction for picture set by emotion, $F(2, 68) = 4.38$, $p = .016$, $\eta_p^2 = .11$. However, there was no main effect for picture set and emotion (both $p > .10$).

3.3.3. Skin conductance response

There were no significant effects for the skin conductance response (all $p > .10$).

3.3.4. Orbicularis activity

Controlling for differences in arousal ratings did not affect the significant main effect for emotion, $F(2, 68) = 3.84$, $p = .035$, $\eta_p^2 = .10$. However, there was no main effect for picture set and no interaction for picture set by emotion (both $p > .10$).

4. Discussion

The present study investigated the hypothesis that according to the motivational theory of emotion (Bradley et al., 2001), pictures of negative, neutral and positive facial expressions and of scenes should elicit comparable patterns of emotional responses. Therefore, we measured valence and arousal ratings, as well as a number of physiological responses, including the startle reflex, heart rate deceleration, skin conductance response, and the activity of the orbicularis oculi EMG.

4.1. Scenes

With respect to pictures of scenes, the results from earlier studies were replicated in the present study (for an example see Bradley et al., 2001). The startle response was modulated by picture valence with lowest amplitudes for positive, intermediate for neutral and greatest amplitudes for negative scenes. Also, the heart rate response varied systematically with picture valence, with greatest deceleration for negative picture contents. This pattern was also evident for the facial EMG of the orbicularis oculi muscle, which is an important component of the Duchenne smile, with the strongest activation during positive scenes. However, skin conductance responses were elevated for threatening picture contents only.

4.2. Faces

The pattern of physiological responses was strikingly different for emotional facial expressions, although the pattern of self-report ratings and orbicularis oculi EMG were comparable between emotional scenes and faces (linear increase in valence ratings, v-shaped in arousal). First of all, we found that the startle amplitude was modulated by picture arousal instead of picture valence. As in negative scenes, amplitudes were clearly potentiated compared to neutral expressions when our participants viewed angry facial expressions of our female actors. This finding in female expressions contradicts previous findings (Hess et al., 2007), but supports others (Springer et al., 2007; Anokhin and Golosheykin, 2009). Furthermore, our finding corresponds with those of other studies showing that female and male anger expressions induce avoidance behavior in the perceiver (Marsh et al., 2005). We found the same startle potentiation when the participants viewed positive facial expressions. Interestingly, high startle responses to happy expressions of female encoders were found in a previous study (Hess et al., 2007).

The response pattern for the orbicularis oculi activity measured by facial EMG was similar for both scenes and faces. They were lowest in response to negative pictures. However, responses were slightly smaller in response to faces than scenes. Heart rate responses to emotional faces were also different from those to scenes – they were not modulated by picture valence. Instead, heart rate deceleration was greatest for neutral facial expressions, as compared to angry and happy expressions. Skin conductance responses were modulated by picture valence instead of arousal, with highest responses to happy expressions.

Taken together, the differing effects of the two motivational systems (Lang, 1995) seemed to be clearly reflected in psychophysiological responses to pictures of complex scenes but not in responses to facial expressions. Instead, several measures indicate that arousal modulated the responses to emotional faces. There are several possible interpretations of the current results.

4.3. Arousal differences between scenes and faces

The heart rate response to neutral faces is not concordant with the startle results we observed. Differing from the often replicated modulation by picture valence in emotional scenes we clearly observed a pattern corresponding with an arousal-modulation of the startle reflex in faces. Interestingly, viewing positive facial expressions lead to an equally potentiated startle response as viewing negative expressions. The interaction of picture set by emotion which was initially significant indicated that startle responses to scenes and facial expressions differed. After controlling for perceived arousal it became clear that this difference was explained by the differences in arousal levels elicited by scenes and faces. However, the highly significant main effect for emotion, indicating that negative stimuli of both sets clearly potentiated the startle response, was not explained by arousal differences. This clearly supports our interpretation that angry expressions posed by female encoders also prime defensive motivation.

Cuthbert et al. (1996) have stated that any startle modulation by emotional scenes as background stimuli can only be observed at sufficiently intense levels of arousal. The threshold they identified for arousal ratings needed (5.5 on a nine point scale) was not met by the mean ratings for emotional facial expressions in the present study but it was met for the emotional scenes where we found the expected modulation (see Table 1). Arousal ratings may be lower in response to faces because emotional responses have waned due to extinction with frequent exposure to all kinds of emotional facial expressions in everyday life, without any consequences. Although extinction has been shown to reduce startle responses due to decreasing arousal (Larson et al., 2000, 2005), we did observe the expected startle potentiation to angry expressions, but we did not find the expected attenuation in response to happy faces. This may indicate that under situations of low perceived arousal, the motivational system selectively supports potentially harmful stimuli, while appetitive behavior may only be initialized when strong reinforcers are present. We have found early behavioral differences when positive and negative faces were viewed as well (Eisenbarth and Alpers, *in press*; Eisenbarth, Gerdes, and Alpers, *in press*). However, it should not be overlooked that there are exceptions from the rule that high arousal is needed for startle attenuation (drug-related cues with low arousal: Geier et al., 2000; Mucha et al., 2000).

4.4. Behavioral relevance

The behavioral relevance of emotional facial expressions portrayed by others may be ambiguous. For example, the valence of a happy face can be easily decoded, and it may lead to emotional activation in the observer. However, motivated behavior can only be effective if it is adequately tuned to situational demands. Because there were no cues to the situational demands when we presented emotional facial expressions, behavioral relevance may not have been obvious. Lang's (1995) emotional priming hypothesis suggests that the appetitive system activates approach behavior when consummation, procreation, or nurturance is the goal and the defensive system activates defense in order to protect the organism from threat. Viewing emotional scenes primes the required behavior, an index of which is the reflex modulation found in previous studies and replicated here. Unlike an emotional scene, a facial expression of happiness in solitude may simply not tell us enough about situational demands in order to prime motivated behavior. On the other hand, emotional expressions of anger are evolutionarily shaped to signal threat and the organism may be tuned to respond to those stimuli automatically (Dimberg and Öhman, 1996), leading to the expected startle potentiation. Rather, the augmented startle response we found when we showed positive facial expressions, may indicate unspecific alertness but not a directionally motivated state. Others have reported arousal-related increases in the eyeblink startle but this was documented in neutral IAPS pictures (Cuthbert et al., 1996). This may suggest that the behavioral relevance of positively valenced facial expressions may be similar to (slightly) arousing neutral pictures of scenes which do not have a clear affective tone.

Taken together, while Cuthbert et al. (1996) suggest that other mechanisms operate at low levels of arousal we simply suggest that the startle modulation found in highly arousing pictures of scenes might be influenced by behavioral relevance derived from context information. When happy faces are presented by themselves and context is not available, the approach systems may not be triggered.

4.5. Attention to neutral faces

The heart rate deceleration was greatest for neutral facial expressions. This suggests that the orienting response to them was greatest. A greater deceleration to neutral compared to positive expressions has been found before (Vrana and Gross, 2004). Orienting to neutral faces may be important because viewers may want to

detect even the slightest hint of an emotional expression in them, while angry or happy expressions are more readily interpreted. This explanation corresponds with another finding in the study of Vrana and Gross (2004) where greater activity of the corrugator muscle was observed in response to neutral facial expressions and interpreted as a sign of greater concentration during encoding. Neutral expressions may represent uncertainty, which could be a cue for non-reward or even punishment (Somerville et al., 2004). Moreover, previous observations suggest that relaxed facial muscles sometimes do not appear to be perfectly neutral although the average of ratings represented in the usual statistics is close to neutral (Alpers and Gerdes, 2007). What was posed as neutral may be interpreted as surprisingly bleak and ambiguous, and their meaning may be less easily decoded than an angry face. This kind of ambiguity may not occur in neutral IAPS pictures of scenes (e.g., that of an ironing board).

4.6. Orbicularis oculi muscle activity

Although the so called Duchenne smile has long been described, the activity of the orbicularis oculi muscle has not been frequently employed in the picture viewing paradigm monitoring responses to IAPS pictures; so far there is no consistent literature. The pattern we found in the orbicularis oculi EMG in response to scenes replicates one prior study (Wolf et al., 2005) and contradicts another (Bradley et al., 2001). In contrast to the study by Bradley et al. (2001), we did not average activity over the complete period of picture presentation but compared the activity during the first three seconds, that is, before the startle probe occurred. The differentiation between negative and positive facial expressions has been documented before (Hess et al., 1998) but these studies have not compared the emotional expressions with neutral expressions as we did in the present study. However, although we found the expected linear trend across emotions, we did not find a significant difference between neutral and negative faces (exploratory analysis). In sum, this study replicates for both kinds of stimuli that the activity of the orbicularis oculi varies with picture valence, and we suggest that recording it can be a meaningful supplement to physiological measures of emotional responding, without the need for additional sensors.

4.7. Emotional input versus emotional output

Faces activate similar brain circuitry as emotional scenes and seem to activate it even more strongly (Britton et al., 2006; Hariri et al., 2002). Emotional faces and scenes have also been shown to be perceived preferentially, e.g., in binocular rivalry (Alpers and Gerdes, 2007; Alpers and Pauli, 2006) and they both strongly lead to attentional engagement (Bradley et al., 1997; Mogg and Bradley, 2002).

Suggestive evidence that both scenes and faces activate brain circuitry responsible for emotional processes such as the amygdala (for reviews see Phan et al., 2004; Zald, 2003) may be related to similar emotional decoding but it should not be over-interpreted as indicating equivalent emotional (i.e. psychophysiological) output. First, the amygdala has several nuclei which differ in their output connections (Pitkänen, 2000) but are difficult to differentiate in humans with current imaging technology (see Merboldt et al., 2001). Second, although amygdala output is directly linked with some of the physiological output which we have measured in the present experiment (Davis and Whalen, 2001; Lang, 1995), other modulatory circuits may well come into play in their modulation. So far, much of what is known about these brain circuits is based on the animal model and still limited to conditioning experiments in the auditory domain. Interestingly, there is a genetic deficit, the Williams–Beuren syndrome, where responses to social cues is clearly dissociated from other potentially fear inducing cues. Patients with this syndrome are uniquely hypersociable but extremely fearful in non-social situations.

This dissociation is reflected in a reduced amygdala activation to emotional facial expressions but increased activation to emotional scenes (Meyer-Lindenberg et al., 2005).

4.8. Limitations

A limitation of our experiment is rooted in the nature of the pictures selected for it. Negative emotional scenes were rated as more arousing than positive scenes, and both emotional scenes were rated as more arousing than the emotional facial expressions (although we statistically controlled for arousal differences). We selected these pictures as being representative for the material used in comparable studies. A meaningful extension of our approach may be to compare facial expressions with scenes matched for valence and arousal ratings. Moreover, presenting negatively-valenced expressions posed by male actors may be a useful variation of our approach. In a large sample this would also allow for further exploration of the interaction of the actors' gender and participants' gender, although this has not been found with respect to self-report measures (e.g., Wild et al., 2001).

That the expected pattern of electrodermal responding was less clear than expected in response to scenes and faces is another limitation of our study. Moreover, it did not remain significant after controlling for arousal differences. However, self-report measures were comparable to normative data for the IAPS, which indicates that our participants responded emotionally to the stimuli and the other channels clearly speak in favor of a valid psychophysiological assessment of responses.

5. Conclusion

To our knowledge, this is the first experiment to directly compare several key psychophysiological responses, previously used in research with scenes and faces, in the classic picture viewing paradigm. Although both, pictures of scenes and faces, are often used to induce emotional states in experimental settings, there are striking differences in the pattern of physiological responses. Our data suggest that the similar activations observed in brain circuitry when these stimuli are processed does not necessarily lead to identical psychophysiological output. In sum, this research suggests that it is very useful to compare different kinds of picture material to further the understanding of how emotional cues are processed and under which conditions they elicit directionally motivated behavior. To understand differences in psychophysiological responses one may need to differentiate between the decoding of emotional input and emotional responses. We hope that this experiment may encourage other researchers to also directly compare physiological and behavioral output between scenes and faces, additional channels such as evoked potentials may be helpful in this endeavor.

Acknowledgements

Georg W. Alpers' and Paul Pauli's work is supported by the Research Group Emotion and Behavior which is sponsored by the German Research Society (DFG). This work is in part based on Dirk Adolph's Master thesis which as supervised by GWA at the department chaired by PP. We thank Heiner Ellgring for the FACS analysis of the facial expressions.

References

Adolph, D., Alpers, G.W., 2010. The Intensity of emotional facial expressions and arousal: differences in two sets of facial expressions. *Am. J. Psychol.* 123, 209–219.

Adolphs, R., 2002. Recognizing emotion from facial expressions: psychological and neurological mechanisms. *Behav. Cogn. Neurosci. Rev.* 1, 21–62.

Alpers, G.W., 2008. Eye-catching: right hemisphere attentional bias for emotional pictures. *Laterality* 13, 158–178.

Alpers, G.W., Gerdes, A.B.M., 2007. Here's looking at you: emotional faces predominate in binocular rivalry. *Emotion* 7, 495–506.

Alpers, G.W., Pauli, P., 2006. Emotional pictures predominate in binocular rivalry. *Cogn. Emot.* 20, 596–607.

Alpers, G.W., Ruhlleder, M., Walz, N., Mühlberger, A., Pauli, P., 2005. Binocular rivalry between emotional stimuli: a validation using conditioned stimuli and EEG. *Int. J. Psychophysiol.* 57, 25–32.

Anokhin, A.P., Golosheykin, S., 2009. Startle modulation by affective faces. *Biol. Psychol.* 83, 37–40.

Azevedo, T.M., Volchan, E., Imbiriba, L.A., Rodrigues, E.C., Oliveira, J.M., Oliveira, L.F., Lutterbach, L.G., Vargas, C.D., 2005. A freezing-like posture to pictures of mutilation. *Psychophysiology* 42, 255–260.

Balaban, M.T., 1995. Affective influences on startle in five-month-old infants: reactions to facial expressions of emotion. *Child Dev.* 66, 28–36.

Blumenthal, T.D., Cuthbert, B.N., Filion, D.L., Hackley, S., Lipp, O.V., van Boxtel, A., 2005. Committee report: guidelines for human startle eyeblink electromyographic studies. *Psychophysiology* 42, 1–15.

Boucsein, W., 1992. *Electrodermal activity*. Plenum Press, New York.

Bradley, B.P., Mogg, K., Millar, N., Bonham-Carter, C., Fergusson, E., Jenkins, J., Parr, M., 1997. Attentional biases for emotional faces. *Cogn. Emot.* 11, 25–42.

Bradley, M.M., Codispoti, M., Cuthbert, B.N., Lang, P.J., 2001. Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion* 1, 276–298.

Bradley, M.M., Moulder, B., Lang, P.J., 2005. When good things go bad: the reflex physiology of defense. *Psychol. Sci.* 16, 468–473.

Britton, J.C., Taylor, S.F., Sudheimer, K.D., Liberzon, I., 2006. Facial expressions and complex IAPS pictures: common and differential networks. *Neuroimage* 31, 906–919.

Cuthbert, B.N., Bradley, M.M., Lang, P.J., 1996. Probing picture perception: activation and emotion. *Psychophysiology* 33, 103–111.

Davis, M., Whalen, P.J., 2001. The amygdala: vigilance and emotion. *Mol. Psychiatry* 6, 13–34.

Dimberg, U., 1982. Facial reactions to facial expressions. *Psychophysiology* 19, 643–647.

Dimberg, U., 1990. Facial electromyography and emotional reactions. *Psychophysiology* 27, 481–494.

Dimberg, U., Öhman, A., 1996. Behold the wrath: psychophysiological responses to facial stimuli. *Motiv. Emot.* 20, 149–182.

Dimberg, U., Petterson, M., 2000. Facial reactions to happy and angry facial expressions: evidence for right hemisphere dominance. *Psychophysiology* 37, 693–696.

Dimberg, U., Thunberg, M., Elmehed, K., 2000. Unconscious facial reactions to emotional facial expressions. *Psychol. Sci.* 11, 86–89.

Ekman, P., Friesen, W., 1982. Felt, false, and miserable smiles. *J. Nonverbal Behav.* 6, 238–252.

Eisenbarth, H., Alpers, G.W., in press. Happy eyes and sad mouth: Scanning emotional facial expressions. *Emotion*.

Eisenbarth, H., Gerdes, A.B.M., Alpers, G.W., in press. Motor-Incompatibility of Facial Reactions: The influence of valence and stimulus content on voluntary facial reactions. *Journal of Psychophysiology*.

Ekman, P., Rosenberg, E.L. (Eds.), 1997. *What the Face Reveals: Basic and Applied Studies of Spontaneous Expression Using the Facial Action Coding System (FACS)*. Oxford University Press, London.

Ekman, P., Sorenson, E.R., Friesen, W.V., 1969. Pan-cultural elements in facial displays of emotion. *Science* 164, 86–88.

Farah, M.J., Wilson, K.D., Drain, M., Tanaka, J.N., 1998. What is "special" about face perception? *Psychol. Rev.* 105, 482–498.

Fridlund, A.J., Cacioppo, J.T., 1986. Guidelines for human electromyographic research. *Psychophysiology* 23, 567–589.

Fydrich, T., 2001. SPAI – Soziale Phobie und Angst Inventar. In: Brähler, E., Schumacher, J., Strauß, B. (Eds.), *Diagnostische Verfahren in der Psychotherapie*. Hogrefe, Göttingen.

Gatchel, R.J., Lang, P.J., 1974. Effects of interstimulus interval length and variability on habituation of autonomic components of the orienting response. *J. Exp. Psychol.* 103, 802–804.

Geier, A., Mucha, R.F., Pauli, P., 2000. Appetitive nature of drug cues confirmed with physiological measures in a model using pictures of smoking. *Psychopharmacology* 150, 283–291.

Graham, F.K., 1997. Afterword: pre-attentive processing and passive and active attention. In: Lang, P.J., Simons, R.F., Balaban, M.T. (Eds.), *Attention and Orienting: Sensory and Motivational Processes*. Erlbaum, Mahaw, NJ, pp. 417–448.

Graham, F.K., Clifton, R.K., 1966. Heart-rate change as a component of the orienting response. *Psychol. Bull.* 65, 305–320.

Hansen, C.H., Hansen, R.D., 1988. Finding the face in the crowd: an anger superiority effect. *J. Pers. Soc. Psychol.* 54, 917–924.

Hariri, A.R., Tessitore, A., Mattay, V.S., Fera, F., Weinberger, D.R., 2002. The amygdala response to emotional stimuli: a comparison of faces and scenes. *Neuroimage* 17, 317–323.

Hess, U., Philippot, P., Blairy, S., 1998. Facial reactions to emotional facial expressions: affect or cognition? *Cogn. Emot.* 12, 509–531.

Hess, U., Sabourin, G., Kleck, R.E., 2007. Postauricular and eyeblink startle responses to facial expressions. *Psychophysiology* 44, 431–435.

Hodes, R.L., Cook, E.W., Lang, P.J., 1985. Individual differences in autonomic response: conditioned association or conditioned fear? *Psychophysiology* 22, 545–560.

Johnsen, B.H., Thayer, J.F., Hugdahl, K., 1995. Affective judgment of the Ekman faces: a dimensional approach. *J. Psychophysiol.* 9, 193–202.

Lang, P.J., 1995. The emotion probe: studies of motivation and attention. *Am. Psychol.* 50, 372–385.

Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O., 1993. Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiology* 30, 261–273.

- Lang, P.J., Bradley, M.M., Cuthbert, B.N., 1997. Motivated attention: affect, activation, and action. In: Lang, P.J., Simons, R.F., Balaban, M.T. (Eds.), *Attention and Orienting: Sensory and Motivational Processes*. Erlbaum, Mahwah, NJ, pp. 97–135.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N., 2005. *International affective picture system (IAPS): affective ratings of pictures and instruction manual*. Technical Report A-6. University of Florida, Gainesville, FL.
- Larson, C.L., Ruffalo, D., Nietert, J.Y., Davidson, R.J., 2000. Temporal stability of the emotion-modulated startle response. *Psychophysiology* 37, 92–101.
- Larson, C.L., Ruffalo, D., Nietert, J.Y., Davidson, R.J., 2005. Stability of emotion-modulated startle during short and long picture presentation. *Psychophysiology* 42, 604–610.
- Laux, L., Schaffner, P., Glanzmann, P., Spielberger, C.D., 1981. *Das State-Trait Angst Angstinventar (STAI)*. Beltz Testgesellschaft, Weinheim.
- LeDoux, J.E., 2000. Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23, 155–184.
- Lee, G.P., Meador, K.J., Loring, D.W., Allison, J.D., Brown, W.S., Paul, L.K., Pillai, J.J., Lavin, T.B., 2004. Neural substrates of emotion as revealed by functional magnetic resonance imaging. *Cogn. Behav. Neurosci.* 17, 9–17.
- Marsh, A.A., Ambady, N., Kleck, R.E., 2005. The effects of fear and anger facial expressions on approach- and avoidance-related behaviors. *Emotion* 5, 119–124.
- Merboldt, K.D., Fransson, P., Bruhn, H., Frahm, J., 2001. Functional MRI of the human amygdala? *Neuroimage* 14, 253–257.
- Merckelbach, H., Van Hout, W., Van den Hout, M.A., Mersch, P.P., 1989. Psychophysiological and subjective reactions of social phobics and normals to facial stimuli. *Behav. Res. Ther.* 27, 289–294.
- Meyer-Lindenberg, A., Hariri, A.R., Munoz, K.E., Mervis, C.B., Mattay, V.S., Morris, C.A., Berman, K.F., 2005. Neural correlates of genetically abnormal social cognition in Williams syndrome. *Nat. Neurosci.* 8, 991–993.
- Mogg, K., Bradley, B.P., 2002. Selective orienting of attention to masked threat faces in social anxiety. *Behav. Res. Ther.* 40, 1403–1414.
- Mucha, R.F., Geier, A., Stuhlinger, M., Mundle, G., 2000. Appetitive effects of drug cues modelled by pictures of the intake ritual: generality of cue-modulated startle examined with inpatient alcoholics. *Psychopharmacology* 151, 428–432.
- Müller, J.L., Sommer, M., Wagner, V., Lange, K., Taschler, H., Roder, C.H., Schuierer, G., Klein, H.E., Hajak, G., 2003. Abnormalities in emotion processing within cortical and subcortical regions in criminal psychopaths: evidence from a functional magnetic resonance imaging study using pictures with emotional content. *Biol. Psychiatry* 54, 152–162.
- Öhman, A., Lundqvist, D., Esteves, F., 2001. The face in the crowd revisited: a threat advantage with schematic stimuli. *J. Pers. Soc. Psychol.* 80, 381–396.
- Phan, K.L., Wager, T.D., Taylor, S.F., Liberzon, I., 2004. Functional neuroimaging studies of human emotions. *CNS Spectr.* 9, 258–266.
- Pitkänen, A., 2000. Connectivity of the rat amygdaloid complex. In: Aggleton, J.P. (Ed.), *The Amygdala: a Functional Analysis*, 2 ed. Oxford University Press, Oxford.
- Russell, J.A., Bullock, M., 1985. Multidimensional scaling of emotional facial expressions: similarity from preschoolers to adults. *J. Pers. Soc. Psychol.* 48, 1290–1298.
- Somerville, L.H., Kim, H., Johnstone, T., Alexander, A.L., Whalen, P.J., 2004. Human amygdala responses during presentation of happy and neutral faces: correlations with state anxiety. *Biol. Psychiatry* 55, 897–903.
- Spangler, G., Emlinger, S., Meinhardt, J., Hamm, A., 2001. The specificity of infant emotional expression for emotion perception. *Int. J. Psychophysiol.* 41, 155–168.
- Springer, U.S., Rosas, A., McGetrick, J., Bowers, D., 2007. Differences in startle reactivity during the perception of angry and fearful faces. *Emotion* 7, 516–525.
- Tottenham, N., Tanaka, J.W., Leon, A.C., McCarry, T., Nurse, M., Hare, T.A., Marcus, D.J., Westerlund, A., Casey, B.J., Nelson, C., 2009. The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Res.* 168, 242–249.
- van Boxtel, A., Boelhouwer, A.J.W., Bos, A.R., 1998. Optimal EMG signal bandwidth and interelectrode distance for the recording of acoustic, electrocutaneous and photic blink reflexes. *Psychophysiology* 35, 690–697.
- Vrana, S.R., Gross, D., 2004. Reactions to facial expressions: effects of social context and speech anxiety on responses to neutral, anger, and joy expressions. *Biol. Psychol.* 66, 63–78.
- Vrana, S.R., Spence, E.L., Lang, P.J., 1988. The startle probe response: a new measure of emotion? *J. Abnorm. Psychol.* 97, 487–491.
- Waters, A.M., Neumann, D.L., Henry, J., Craske, M.G., Ornitz, E.M., 2008. Baseline and affective startle modulation by angry and neutral faces in 4–8-year-old anxious and non-anxious children. *Biol. Psychol.* 78, 10–19.
- Whalen, P.J., 1998. Fear, vigilance, and ambiguity: initial neuroimaging studies of the human amygdala. *Curr. Dir. Psychol. Sci.* 7, 177–188.
- Whalen, P.J., Rauch, S.C., Etcoff, N.L., McInerney, S.C., Lee, M.B., Jenike, M.A., 1998. Masked Presentations of Emotional Facial Expressions Modulate Amygdala Activity without Explicit Knowledge. *J. Neurosci.* 18, 411–418.
- Whalen, P.J., Kagan, J., Cook, R.G., Davis, F.C., Kim, H., Polis, S., McLaren, D.G., Somerville, L.H., McLean, A.A., Maxwell, J.S., Johnstone, T., 2004. Human amygdala responsivity to masked fearful eye whites. *Science* 306, 2061.
- Wild, B., Erb, M., Bartels, M., 2001. Are emotions contagious? Evoked emotions while viewing emotionally expressive faces: quality, quantity, time course and gender differences. *Psychiatry Res.* 102, 109–124.
- Wolf, K., Mass, R., Ingenbleek, T., Kiefer, F., Naber, D., Wiedemann, K., 2005. The facial pattern of disgust, appetite, excited joy and relaxed joy: an improved facial EMG study. *Scand. J. Psychol.* 46, 403–409.
- Zald, D.H., 2003. The human amygdala and the emotional evaluation of sensory stimuli. *Brain Res. Rev.* 41, 88–123.