Research Report

Emotions in motion: Dynamic compared to static facial expressions of disgust and happiness reveal more widespread emotion-specific activations[☆]

Sina Alexa Trautmann[a,*], Thorsten Fehr[a,b,c], Manfred Herrmann[a,b]

[a]Department of Neuropsychology and Behavioral Neurobiology, Center for Cognitive Sciences, University of Bremen, Hochschulring 18, D-28359 Bremen, Germany
[b]Center for Advanced Imaging (CAI), University of Bremen, Germany
[c]Department of Neurology, Otto-von-Guericke-University Magdeburg, Germany

ARTICLE INFO

ABSTRACT

In social contexts, facial expressions are dynamic in nature and vary rapidly in relation to situational requirements. However, there are very few fMRI studies using dynamic emotional stimuli. The aim of this study was (1) to introduce and evaluate a new stimulus database of static and dynamic emotional facial expressions according to arousal and recognizability investigated by a rating by both participants of the present fMRI study and by an external sample of 30 healthy women, (2) to examine the neural networks involved in emotion perception of static and dynamic facial stimuli separately, and (3) to examine the impact of motion on the emotional processing of dynamic compared to static face stimuli. A total of 16 females participated in the present fMRI study performing a passive emotion perception task including static and dynamic faces of neutral, happy and disgusted expressions. Comparing dynamic stimuli to static faces indicated enhanced emotion-specific brain activation patterns in the parahippocampal gyrus (PHG) including the amygdala (AMG), fusiform gyrus (FG), superior temporal gyrus (STG), inferior frontal gyrus (IFG), and occipital and orbitofrontal cortex (OFC). These regions have been discussed to be associated with emotional memory encoding, the perception of threat, facial identity, biological motion, the mirror neuron system, an increase of emotional arousal, and reward processing, respectively. Post hoc ratings of the dynamic stimuli revealed a better recognizability in comparison to the static stimuli. In conclusion, dynamic facial expressions might provide a more appropriate approach to examine the processing of emotional face perception than static stimuli.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Emotions play an important role in regulating social behavior (see Adolphs, 2002 for review). The impact of emotions on our thoughts, memory, attention, decisions and behavior is part of everyday life experience. Everyday social life requires correct perception and interpretation of different emotional facial expressions for adequate behavior in social contexts.

Pioneering work in the study of face and emotional face perception was provided by Bruce and Young (1986). Based on this face perception model, Haxby et al. (2000) modified the latter model. This modified model is based on a "core" and an "extended system" of face perception. The "core system" represents the visual analysis of faces and comprises the inferior occipital gyri for early visual analysis, the fusiform face area (FFA) for the processing of facial features and identity, and the superior temporal sulcus (STS) area for the processing of changeable facial features (i.e., eyes, mouth, expressions; see also Allison et al. (2000), for review). The "extended system" is reciprocally linked to the core system and comprises the auditory cortex (i.e., for lip reading), parietal areas (i.e., for spatial attention to changeable features), the temporal pole (TP, associated with autobiographical information, names, and personal identity), and the amygdala (AMG, emotion, facial expressions). Haxby et al. claimed that the temporal sequence of processing of the different stages of the model should be addressed in detail in future studies (Haxby et al., 2000). Adolphs (2002) focused on this aspect and extended the face perception model by Haxby et al. (2000) by adding the temporal dimension of face and emotion perception and recognition. Within the first 120 ms after emotion onset, the amygdala (AMG, at this point, the AMG is activated in the early processing stage), the striate cortex and the thalamus are proposed to process and encode automatically very early perceptual structures of salient emotional stimuli. This is considered to be equivalent to the "core system" as suggested by Haxby et al. (2000).

The equivalent of the "extended system" of emotion recognition modules according to Adolphs (2002) comprises the striate cortex, the fusiform face area (FFA; early), the superior temporal gyrus (STG; early), the AMG, late (reactivation of the AMG), the orbitofrontal cortex (OFC) and the basal ganglia (BG). The latter regions are proposed to play a role in processing the motion of emotional expressions, even if simply implied by static stimuli (superior temporal sulcus [STS] area, especially for changes in mouth and eye area; for review, see Allison et al. (2000); Haxby et al. (2000); Hoffman and Haxby (2000)).

Numerous fMRI studies have provided evidence for an involvement of emotion-related neural networks in the perception of static emotional face expressions (for review, see Adolphs (2002); Davidson and Irwin (1999); LeDoux (1996); Murphy et al. (2003); Phan et al. (2002)).

The majority of emotion perception studies (for reviews, see Adolphs (2002); Davidson and Irwin (1999); Murphy et al. (2003); Phan et al. (2002)) have used stimuli displaying static emotional facial expressions (see also Ekman and Friesen, 1976). Natural features, however, should better be considered for stimulus construction because they convey an increased richness of temporal and structural facial object properties (Harwood et al., 1999; Sato et al., 2004), which can improve the three-dimensional perception of faces (Knight and Johnston, 1997). These features, in turn, potentially facilitate emotion recognition and might even support the processing of social interactions in a more natural way (Bassili, 1979; Berry, 1990; LaBar et al., 2003; Sato et al., 2004).

Behavioral studies on moving facial expressions corroborate this line of argumentation and showed higher arousal rates (Simons et al., 1999; Weyers et al., 2006, respectively) as well as better recognition accuracy (Ambadar et al., 2005; Bassili, 1979; Harwood et al., 1999) during rating tasks of dynamic compared to static emotional facial expressions.

To date, there are only few neuroimaging studies addressing the perception of dynamic emotional stimuli, and, to our knowledge, there is no fMRI study examining the neural processing of dynamic facial expressions of disgust.

In a PET study, Kilts et al. (2003) contrasted dynamic and static emotional face stimuli showing happy and angry facial expression. They reported increased activity in V5, STS area and periamygdaloid area for dynamic versus static angry faces and cuneus, V5, lingual, middle temporal and medial frontal gyrus for dynamic versus static happy faces. In an fMRI study, LaBar et al. (2003) presented photographs and morphed videos of emotional expressions of anger and fear and reported an enhancement of activation for emotional compared to neutral expressions in – among other – the fusiform gyrus (FG), the ventromedial prefrontal (also orbitofrontal) cortex and the STS area for dynamic stronger than for static faces. Sato et al. (2004) applied a passive viewing task including happy and fearful dynamic faces. They described more widespread activations for dynamic compared to static facial expressions in happy and fearful expressions when compared to neutral faces or mosaics of scrambled faces. In line with the work of Kilts et al. (2003) and Labar et al. (2003), Sato et al. (2004) concluded that dynamic stimuli convey more lively and realistic aspects of faces occurring in social interactions and related those to leading to more widespread activation patterns.

The above-mentioned studies demonstrated that the processing of dynamic in contrast to static facial expressions appear to more reliably recruit neural networks of emotion processing such as the amygdala (Kilts et al., 2003; LaBar et al., 2003), fusiform gyrus, inferior occipital, middle and superior temporal regions (STS area; for reviews, see Allison et al. (2000); Haxby et al. (2000)), motion sensitive areas (MT+/V5), and the lateral inferior frontal cortex (mirror neuron system; Buccino et al., 2001; Kilts et al., 2003; LaBar et al., 2003; Leslie et al., 2004; Sato et al., 2004).

We presume that natural moving faces might provide a more valid stimulus basis for the examination of neuronal correlates of facial expression perception. Only few studies have applied "natural" dynamic facial expressions (Gepner et al., 2001; Kilts et al., 2003). Kilts et al. (2003) applied dynamic emotional expressions of neutrality, happiness, and anger of a face database, which consisted of each two female and two male professional actors. Gepner et al. (2001) have recorded videos of one actress displaying natural dynamic facial expressions of joy, surprise, sadness, disgust, by exclusively one actress. The downside of those studies is that study participants might have run the risk of habituation because the same actors were presented multiple times. For this reason, we developed a new stimulus data set based on 80 different amateur actors and actresses.

The present study aimed at three central points: First, since we used a new stimulus database, the stimuli needed to be evaluated (i) by an extensive psychometrical evaluation study (see Experimental procedures section), and (ii) by participants of the fMRI study. Second, BOLD activation patterns of

emotional (happiness/disgust) compared to neutral faces were examined. The above discussed network of emotion-specific areas of emotional (happiness/disgust) compared to neutral faces was expected for both static and dynamic stimuli. Third, we examined BOLD activation patterns of dynamic compared to static stimuli of both emotional valences compared to neutrality. We expected an "emotion by motion effect" which refers to the enhancement of emotional face perception and of activation of the above-mentioned emotion-specific network by the movement of emotional facial expressions. Thus, we expected consistent (i.e., reliable) and more widespread (i.e., topographically larger distributed) activation patterns for dynamic faces in the above-mentioned emotion-specific network compared to static stimuli. Besides, this enhanced "emotion by motion" effect should also result in a better recognition rate of the different facial expressions in dynamic compared to static stimuli on a behavioral level.

2. Results

2.1. Behavioral data (evaluation study)

Data of the behavioral evaluation study of 30 healthy female participants (mean age 22.7±2.9 years, see Experimental procedures for further information) showed a recognition accuracy rate of 94.1% (±9.8) for neutral, 98.1% (±5.2) for happy, 94.2% (±4.5) for disgust, 95.3% (±6.4) for fearful, and 88.8% (±5.1) for angry expressions. Repeated measurement ANOVAs with the factor EMOTION (5 levels: neutrality, happiness, disgust, fear, anger), calculated for arousal and category separately, revealed significant main effects of EMOTION for both category ($F_{[2.5, 72.1]}=10.2$, $p<.001$, Greenhouse Geisser (GG) corrected) and arousal ($F_{[1.8, 52.2]}=23.6$, $p<.001$, GG corrected) explained by a higher recognition rate of happy

Table 1 – Contrasts: disgust>neutral for each the dynamic and static modality.

	Brain area	BA	Dynamic faces: disgust>neutral					BA	Static faces: disgust>neutral				
			x	y	z	T-value	k		x	y	z	T-value	k
	Occipital												
R	Tuber		24	−83	−29	4.23	48						
	Parietal												
L	Supramarginal Gyrus	40	−53	−41	35	5.68	67						
	Temporal												
L	Superior Temporal Gyrus	39	−50	−53	21	8.10	1392						
L	Middle Temporal Gyrus	37	−40	−64	9	6.76							
L	Middle Temporal Gyrus	39	−51	−69	13	6.40							
L	Fusiform Gyrus	37	−42	−43	−15	6.92	125						
R	Middle Temporal Gyrus	37	55	−66	3	10.66	617						
R	Middle Occipital Gyrus	19	55	−68	−5	7.44							
R	Middle Temporal Gyrus	19	50	−79	9	4.09							
R	Superior Temporal Gyrus	22	67	−44	13	8.46	86						
R	Supramarginal Gyrus (parietal)	40	67	−43	28	4.21							
R	Superior Temporal Gyrus	22	46	−35	5	4.93	157						
R	Uncus	34	18	1	−20	6.51	303						
R	Superior Temporal Gyrus	38	28	7	−24	6.12							
R	Uncus	36	22	−5	−30	5.17							
	Frontal												
L	Medial Frontal Gyrus	9	−10	44	25	4.23	22						
L	Inferior Frontal Gyrus	45	−55	18	6	5.75	556						
L	Inferior Frontal Gyrus	47	−57	17	−6	5.67		45	−46	27	2	4.28	207
L	Inferior Frontal Gyrus	45	−59	22	12	5.09		45	−46	24	17	4.28	
L	Middle Frontal Gyrus							46	−53	30	21	4.07	
R	Superior Frontal Gyrus	6	6	15	62	6.28	416						
L	Superior Frontal Gyrus	6	0	5	61	5.25		6	−2	5	53	3.9	
L	Superior Frontal Gyrus	6	−2	17	60	4.95							
R	Middle Frontal Gyrus	9	59	12	36	4.47	32						
R	Middle Frontal Gyrus	6	55	4	40	4.09							
R	Inferior Frontal Gyrus	44	63	9	16	6.47	60						
	Subcortical												
L	Uncus	38	−24	4	−34	6.90	363						
L	Amygdala		−20	−6	−13	6.24							
L	Putamen								−20	4	0	3.43	21
R	Parahippocampal Gyrus	34	20	−12	−13	5.26	45						
R	Posterior Cingulate	29	0	−54	12	4.59	33						
R	Mammillary Body		4	−12	−11	4.60	40						

Talairach coordinates of simple BOLD contrasts ($p<.001$, uncorrected, $k=20$) of dynamic (disgust>neutral) and static (disgust>neutral) facial expressions. *Italic=lowered statistical threshold for explorative purposes: $p<.005$, uncorrected, $k=20$.*

compared to neutral (p=.049), disgusted (p=.005), fearful (p=.002), and angry (p<.001) faces and a better recognition rate of neutral, disgusted and fearful faces compared to angry faces (p=.002, p<.001, p<.001, respectively). Happy faces (mean arousal rating: 6.5±1.3) showed a higher arousal compared to faces of neutrality (p<.001; mean 4.4±1.7), disgust (p=.02; mean 5.9±1.7), fear (p<.001; mean 5.6±1.6), and anger (p<.001; mean 5.0±1.5), faces of disgust showed higher arousal compared to neutrality (p<.001), fear (p=.046), and anger (p<.001), and fearful facial expressions showed a higher arousal compared to neutral (p=.001) and angry ones (p<.001).

In conclusion, the evaluation study revealed a respectably high recognition accuracy which was also supported by the behavioral data of the fMRI study.

2.2.　Behavioral data (fMRI study)

Post hoc evaluation of the facial expression stimuli revealed a recognition rate for the static stimuli of 98.0% (±3.9) for neutral, 97.8% (±3.4) for happy, and 97.5% (±2.0) for disgusted facial expressions, and for the dynamic stimuli of 95.9% (±8.7) for neutral, 99.5% (±1.4) for happy, and 98.9% (±2.0) for disgusted expressions. A MODALITY (2 levels: static and dynamic)×EMOTION (three levels: happy, disgusted, and neutral)×SEQUENCE (2 levels: start with static or start with dynamic stimuli) repeated measurement ANOVA, separately conducted for the category and arousal ratings, revealed a significant EMOTION×MODALITY interaction ($F_{[1.5, 20.6]}$=3.7, p=.05, GG corrected) for category. This effect was explained by a significantly higher recognition rate for dynamic compared to static disgusted facial expressions (post hoc t-test, p=.01), and by a trend for better recognition rate for dynamic compared to static happy facial expressions (post hoc t-test, p=.07).

Arousal showed a main effect for EMOTION ($F_{[2, 28]}$=11.08, p<.001) resulting in higher arousal rates for emotional expressions independent from motion and a trend for MODALITY ($F_{[1, 14]}$=4.26, p=.058) yielding higher arousal rates for dynamic compared to static stimuli independent of emotion. However, the EMOTION×MODALITY interaction did not reach significance ($F_{[2, 28]}$=1.8, p<.18).

2.3.　FMRI data

We observed significantly stronger activations for static facial expressions of disgust compared to neutral ones in left inferior (BA 45) and middle (BA 46) frontal gyrus (see Table 1, Fig. 1A, lower row). To check for further emotion-related activated regions at a lower statistical threshold, the
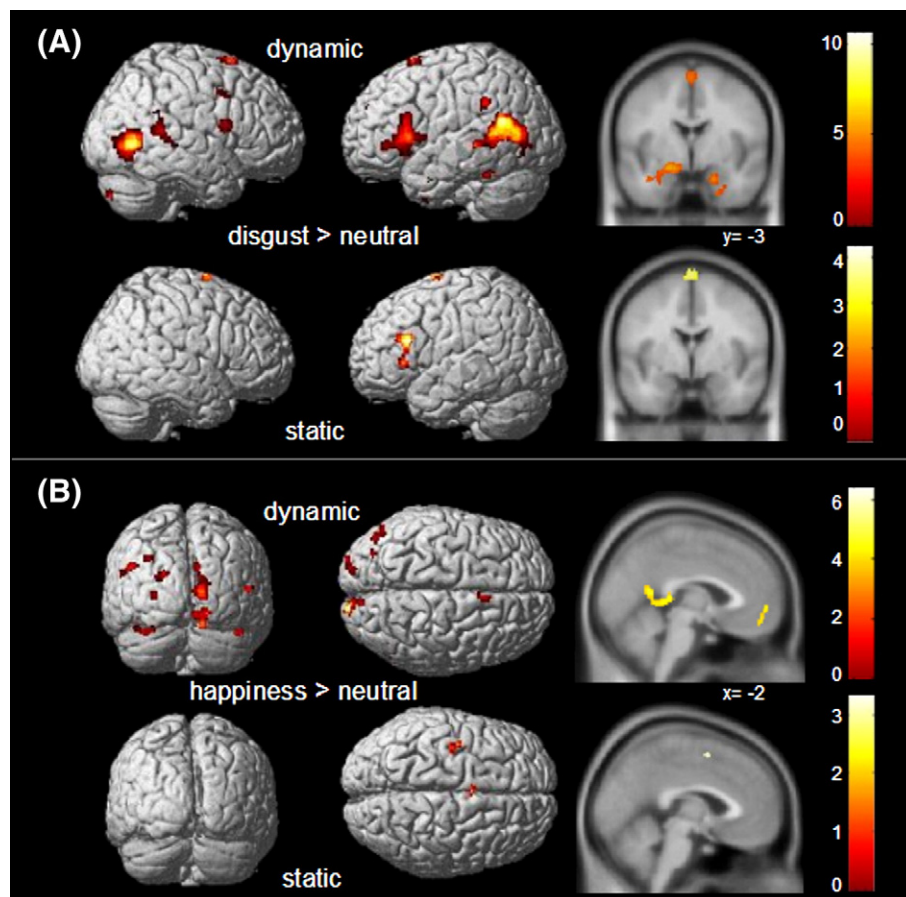

Fig. 1 – Contrasts of emotional compared to neutral facial expressions (p<.001, uncorrected, k=20) show stronger and more widespread emotion-specific activations. (A) Emotion effect of disgust for the dynamic (upper row) and static modality (lower row, here p<.005 for explorative purposes, uncorr., k=20). (B) Emotion effect for happiness for the dynamic (upper row) and static modality (lower row, here p<.005 for explorative purposes, uncorr., k=20).

significance level was decreased to $p<.005$ (uncorrected, $k=20$) for explorative purposes and revealed additional, significant activation in left medial superior frontal gyrus (BA 6) and left Putamen (see Table 1, additional regions are displayed in italic).

Comparing happy to neutral static expressions displayed no activity on the whole-brain basis with the set threshold of $p<.001$ (uncorrected, $k=20$). A reduction of the significance level to $p<.005$ (uncorrected, $k=20$) for explorative purposes resulted in significant activation in the left medial superior frontal gyrus, the left lateral precentral gyrus (all BA 6, see Table 2, additional regions are displayed in italic, Fig. 1B, lower row) and the right cerebellar tonsil.

Fig. 1 (upper row) also depicts the emotion effects of dynamic facial stimulus conditions ($p<.001$, uncorrected, $k=20$). Disgusted in contrast to neutral dynamic facial

expressions resulted in bilateral inferior frontal, right middle frontal (premotor area, PMA), left medial frontal, bilateral superior frontal areas (supplementary motor area, SMA), right posterior cingulate cortex (PCC), bilateral supramarginal regions, in left fusiform gyrus (FG, FFA), and in bilateral superior and middle temporal regions (STS area; see also Table 1 and Fig. 1A, upper row). Furthermore, disgusted vs. neutral dynamic facial expression stimuli showed an activation pattern comprising right parahippocampal gyrus (PHG), left uncus, and the amygdala (AMG; see Fig. 1A, upper row and Table 1 for further details).

Comparing happy to neutral dynamic facial expressions resulted in a signal increase in right superior frontal gyrus, left medial frontal gyrus (spreading medially and ventrally to OFC), right posterior FG, left FG (FFA), bilateral middle temporal gyrus (MTG, STS area) posterior, left angular gyrus

	Brain area	BA	Dynamic faces: happy>neutral					BA	Static faces: happy>neutral				
			x	y	z	T-value	k		x	y	z	T-value	k
	Occipital												
L	Middle Occipital Gyrus	18	−26	−97	10	4.64	23						
L	Declive (range 9 mm)	19	−34	−73	−18	4.42	49						
L	Fusiform Gyrus	19	−42	−78	−15	4.33							
L	Fusiform Gyrus	19	−26	−80	−16	4.05							
L	Cuneus	19	−18	−92	27	4.56	40						
R	Lingual Gyrus	17	16	−90	−4	6.44	143						
R	Declive	18	14	−78	−11	5.24							
R	Lingual Gyrus	18	18	−82	−6	3.90							
R	Fusiform Gyrus	19	46	−67	−17	4.59	33						
R	Cuneus	18	14	−95	10	5.85	165						
R	Cuneus	19	12	−94	23	4.27							
R	Cuneus	19	10	−84	30	4.34	25						
	Parietal												
L	Precuneus	19	−32	−74	37	4.36	20						
L	Supramarginal Gyrus												
	Temporal												
L	Fusiform Gyrus	37	−42	−57	−16	4.43	39						
L	Culmen	37	−36	−55	−21	4.17							
L	Angular Gyrus	39	−44	−74	31	4.79	59						
L	Middle Temporal Gyrus	39	−53	−67	25	4.15							
R	Middle Temporal Gyrus	19	51	−62	12	5.12	26						
	Frontal												
L	Medial Frontal Gyrus	10	−4	52	−4	4.44	61						
L	Medial Frontal Gyrus	11	−2	48	−14	4.07							
L	Superior Frontal Gyrus							6	−2	5	51	3.22	25
L	Precentral Gyrus							6	−40	−5	61	3.37	29
L	Precentral Gyrus							6	−38	−12	63	3.24	
R	Superior Frontal Gyrus	6	4	21	63	5.86	49						
	Cerebellum												
R	Cerebellar Tonsil								26	−56	−38	3.35	28
R	Cerebellar Tonsil								20	−64	−34	3.28	
	Subcortical												
L	Extra-Nuclear/Claustrum		−28	18	8	4.92	24						
L	Hippocampus		−28	−29	−7	6.40	83						
L	Parahippocampal Gyrus	28	−18	−28	−10	6.22							
R	Parahippocampal Gyrus	30	18	−43	4	6.33	631						
R	Posterior Cingulate	30	16	−50	8	6.19							
R	Posterior Cingulate	29	4	−52	12	5.51							

Table 2 – Contrasts: happy>neutral for each the dynamic and static modality.

Talairach coordinates of BOLD contrasts ($p<.001$, uncorrected, $k=20$) of dynamic (happy>neutral) and static (happy>neutral) facial expressions. *Italic=lowered statistical threshold for explorative purposes: $p<.005$, uncorrected, $k=20$.*

including parts of the middle temporal gyrus (STS area), right PCC, bilateral PHG, left precuneus, and occipital brain regions (see Table 2 and Fig. 1B, upper row).

Interaction analysis including the contrasts disgusted vs. neutral expressions for each static and dynamic stimuli revealed larger activation differences for dynamic compared to static stimuli in left rectal gyrus (OFC), left inferior frontal gyrus (PMA), left superior temporal gyrus (STG), bilateral middle temporal gyri (STS area), left inferior temporal gyrus (lateral FFA), and right middle occipital gyrus (MOG, spreading to MT+/V5, see Table 3 and Fig. 2A, for further details). Furthermore, dynamic disgusted facial expressions showed larger bilateral differences in parahippocampal gyrus (PHG) comprising the uncus and amygdala (see Table 3 and Fig. 2A, left column, for further details). Mean percent signal change revealed an enhanced signal for dynamic disgusted facial expressions compared to static and dynamic faces of happy and neutral valence in left inferior frontal gyrus (IFG), right MTG (STS area), left lateral inferior temporal gyrus (FFA), and left AMG (see Fig. 2A, left column). Activations of the left

rectal gyrus and the right MOG did not reach statistical significance in the simple contrasts above for dynamic disgust perception (see Fig. 1A and Table 1). Consequently, a further interaction analysis revealed additional emotion-specific regions and thus revealed brain regions which were specifically enhanced by both disgust and the dynamic modality.

Interaction analysis based on the happy vs. neutral contrasts for both static and dynamic stimuli showed larger differences for dynamic compared to static stimuli in left inferior frontal (IFG, part of the OFC) and subcallosal gyrus, left medial anterior STG, left anterior middle temporal gyrus (both anterior temporal pole), left posterior inferior temporal gyrus (ITG, FFA), left precuneus comprising the superior and inferior parietal lobule, right cuneus, and right middle occipital gyrus (comprising MT+/V5 and STS area, see Table 3, Fig. 2B, for details). Corresponding percent signal change data support a stronger signal increase for the dynamic happy facial expressions compared to the static condition in ventromedial and subcallosal regions, right middle occipital gyrus (including

	Brain area	BA	Interaction: dynamic faces (disgust>neutral)>static faces (disgust>neutral)					BA	Interaction: dynamic faces (happy>neutral)>static faces (happy>neutral)				
			x	y	z	T-value	k		x	y	z	T-value	k
	Occipital												
R	Middle Occipital Gyrus	18	28	−82	1	3.73	26						
R	Middle Occipital Gyrus (V5/MT+)							19	51	−70	7	3.89	27
R	Middle Occipital Gyrus	18	20	−89	15	3.68	28						
R	Middle Occipital Gyrus	18	22	−96	23	3.51							
R	Cuneus							18	12	−96	21	4.28	166
R	Cuneus							19	26	−92	27	3.97	
R	Cuneus							19	12	−94	29	3.89	
	Temporal												
	Superior Temporal Gyrus	39	−51	−53	21	4.52	73	38	−38	16	−23	3.96	23
L	Middle Temporal Gyrus	22	−57	−35	2	3.90	69	21	−55	1	−27	4.39	21
L	Inferior Temporal Gyrus	37	−44	−43	−15	4.19	98	37	−46	−44	−16	4.20	45
R	Middle Temporal Gyrus	21	61	−60	9	4.83	312						
R	Middle Occipital Gyrus (V5/MT+)	19	53	−68	7	4.70							
R	Middle Temporal Gyrus	37	42	−62	10	3.79							
R	Middle Temporal Gyrus	21	55	−8	−13	4.13	35						
	Parietal												
L	Precuneus							19	−32	−74	37	4.13	27
	Frontal												
L	Middle Frontal Gyrus	8	−24	23	36	4.22	21						
L	Medial Frontal Gyrus							10	−4	45	12	3.83	28
L	Rectal Gyrus	11	−10	34	−20	4.12	28						
L	Sub-lobar								−6	7	−7	3.75	56
L	Subcallosal Gyrus							25	−6	19	−14	3.66	
L	Inferior Frontal Gyrus	45	−55	18	8	3.88	31	25	−12	32	−17	3.83	76
L	Inferior Frontal Gyrus	45	−59	24	12	3.53		11	−20	32	−18	3.75	
R	Middle Frontal Gyrus	9	59	12	36	4.47	32						
	Subcortical												
L	Parahippocampal Gyrus/AMG	34	−12	−1	−13	5.43	1139						
R	Parahippocampal Gyrus/AMG	34	20	−12	−15	5.37							
L	Uncus	28	−22	9	−21	5.08							
L	Hypothalamus								−4	−3	−12	4.67	42

Table 3 – Interaction: dynamic faces>static faces.

Talairach coordinates of dynamic versus static stimuli (interaction analysis, $p<.001$, uncorrected, $k=20$) for disgust ([dynamic disgust>dynamic neutral]>[static disgust>static neutral]) and happiness ([dynamic happy>dynamic neutral]>[static happy>static neutral]).
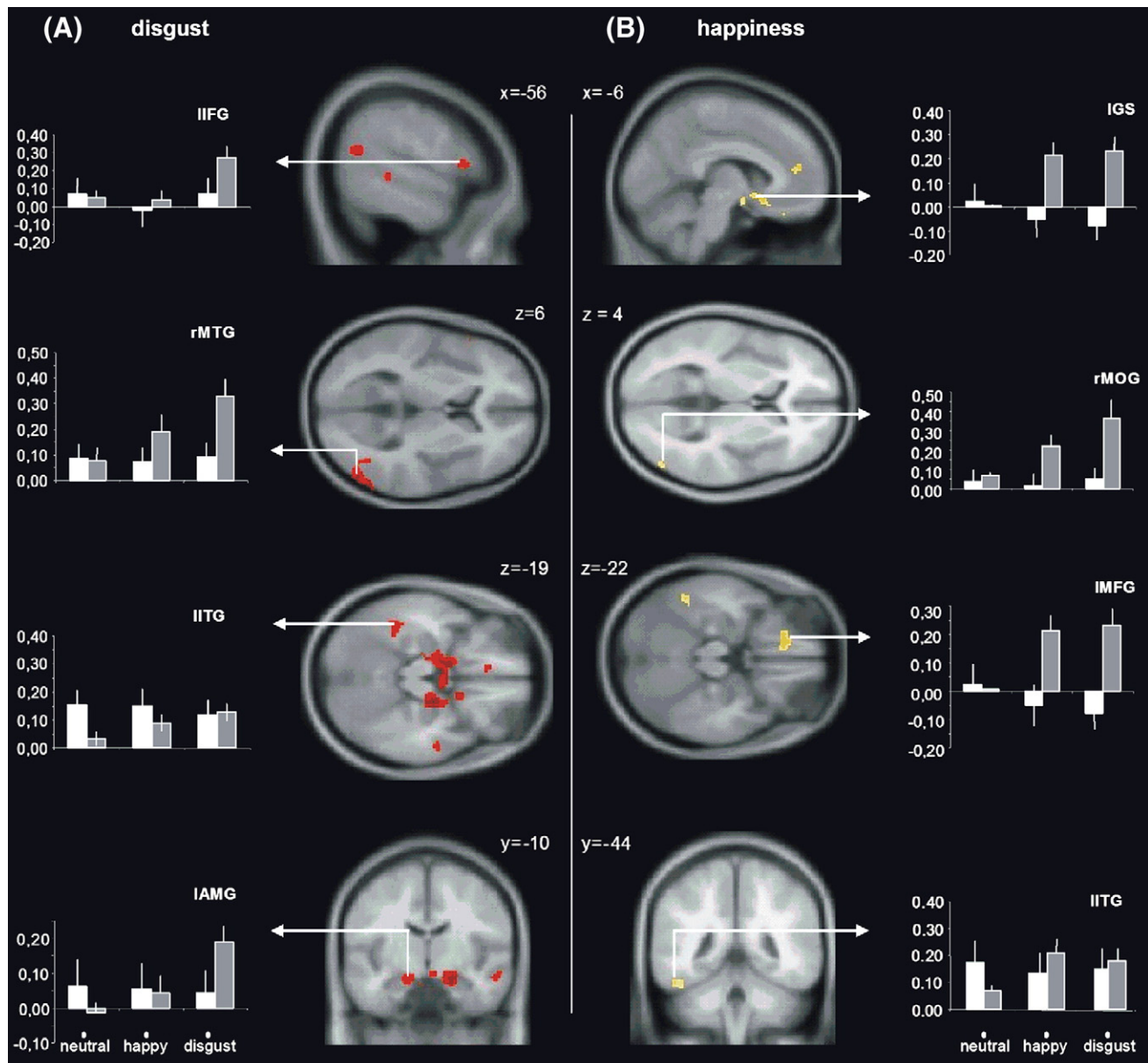
Fig. 2 – Interaction analysis (*p*<.001, *k*=20) shows an enhanced emotion by motion effect for (A) disgust ([dynamic disgust>dynamic neutral]>[static disgust>static neutral] in left inferior frontal gyrus (lIFG), right middle temporal gyrus (rMTG,→STS area), left inferior temporal gyrus (lITG,→FFA) and left amygdala (lAMG), and (B) happiness ([dynamic happy>dynamic neutral]>[static happy>static neutral] in left subcallosal gyrus (lGS), right middle occipital gyrus (rMOG, including MT+/V5 and STS), left medial frontal gyrus (lMFG), and left inferior temporal gyrus (lITG, including fusiform face area (FFA)). Percent signal change graphs were derived from the Marsbar toolbox (http://marsbar.sourceforge.net). Bright bars indicate the static stimulus condition (±1 standard error of mean (SEM)), grey bars show the dynamic stimulus condition (±1 SEM).

MT+ and STS area) and left inferior temporal gyrus (FFA, see Fig. 2B).

Activations of the left inferior frontal and subcallosal gyrus (OFC) and the left anterior temporal Pole did not reach statistical significance in the simple contrasts above for happy compared to neutral stimuli (see Fig. 1B and Table 2). Consequently, the interaction analysis revealed additional emotion-specific regions and thus revealed brain regions which were specifically enhanced by both happiness and the dynamic modality.

3.   Discussion

In the present study, we aimed at two central hypotheses. First, we predicted that the processing of the emotional facial expressions of a newly introduced stimulus database would evoke emotion-specific networks. Second, we expected more widespread BOLD activation patterns for dynamic compared to static facial expressions in those emotion-specific regions

and a higher recognition accuracy of emotional stimuli for the dynamic modality.

Confirming the above-mentioned hypotheses for the largest part, an emotion-specific brain activation pattern was shown to be involved in the processing of dynamic facial expressions of both disgust and happiness. Commonly activated areas for static and dynamic facial emotional expressions referred to the SMA and inferior frontal regions. The present study revealed a wider network of brain regions for dynamic facial expressions compared to static ones involved in emotion perception, like, e.g., the AMG (for disgust only), the parahippocampal regions, the striate and extra-striate areas, the FFA, the STS area, the OFC, and the SMA and the PMA for both emotional valences. Besides, this emotion-specific network has also been shown to be enhanced by motion for the dynamic compared to static stimulus modality confirming our second hypothesis. Furthermore, ratings of the stimulus material confirmed a higher recognition accuracy of dynamic compared to static stimuli.

Besides, as far as we know, this was the first study presenting 40 different natural dynamic facial expressions for 3 different emotional categories. Previous studies investigating dynamic emotion perception used either (1) stimuli consisting of computer generated faces (Krumhuber and Kappas, 2005) or morphed stimuli which were either constructed on the basis of static stimuli (e.g., the face inventory introduced by Ekman and Friesen (1976); see also, Sato et al. (2004)) running the risk of non-natural and artificial motion perception or used (2) only one or two different actors displaying different emotional expressions and thus running the risk of habituation (see, e.g., Gepner et al., 2001; Kilts et al., 2003).

However, there were two surprising findings: first, this emotion-specific network could not be shown as reliably activated for static stimuli as it could for dynamic stimuli. Second, we did not show insula activation for disgust perception. In the following these results will be discussed in more detail.

3.1. Emotional stimulus processing

Emotion perception has been extensively described in previous studies and a network of anatomical regions such as visual areas, FFA, STS region, amygdala, orbitofrontal cortex, premotor as well as inferior frontal areas have been shown to take part in processing, analyzing and evaluating emotional face stimuli (for review, see Adolphs (2002); Phan et al. (2002)). These brain regions are known to subserve multiple emotional and cognitive functions.

3.2. Striate and extrastriate areas

Striate and extrastriate areas have been attributed to early stages of visual processing (Kilts et al., 2003), and their enhanced activation would index more selective attention in emotional compared to neutral stimuli due to an increase of arousal (Kosslyn et al., 1996; Lane et al., 1997; Phillips et al., 1997; Schienle et al., 2002) emphasizing the interaction of emotion and attention in posterior brain regions. An increase of arousal for dynamic emotional faces has previously been described in behavioral studies (Simons et al., 1999; Weyers et al., 2006).

In the present study, participants watched the emotional faces passively (without executing a button press). This might have triggered (1) arousal as indicated by corresponding behavioral data showing higher arousal values for emotional compared to neutral faces and (2) neuronal activation in posterior visual areas (MOG) for both emotional valences compared to neutrality. Besides, behavioral data showed increased arousal rates for the dynamic modality independent of emotion explaining the enhanced neuronal activation of the MOG for both disgust and happiness as revealed by the interaction analyses.

3.3. FFA and STS area

Another aspect of dynamic face perception includes the perception of (1) structural details, such as identity, and (2) moving characteristics of the perceived faces, such as the changing muscular configuration during the development of an emotional expression. The inferior temporal and fusiform gyrus (e.g., FFA) have been discussed to be involved in faces identification (Grill-Spector et al., 2004; Haxby et al., 2000; Hoffman and Haxby, 2000; Kanwisher et al., 1997) and – in more detail – the detection, encoding and/or analysis of invariant facial features such as eyes, mouth, and nose (Halgren et al., 1999). Furthermore, activation of FFA was reported in many studies addressing attentional demands in the context of emotion perception (Narumoto et al., 2001; Pessoa et al., 2002; Vuilleumier et al., 2001, 2004), and motion processing of dynamic facial expressions (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). According to our hypotheses, FFA activity was enhanced by emotional salience of both disgusted and happy stimuli, hence emotion per se, and was moreover enhanced by dynamic characteristics in both valences. We suggest that the FFA might be modulated by emotional characteristics of faces and recruit more attentional resources in dynamic compared to static stimuli resulting in more widespread activation patterns. Again, this line of argumentation might be in line with the generally higher arousal rates for the dynamic stimulus modality compared to the static modality.

The perception of movement in a face plays an important role for emotional face perception. We found STS area activation for happiness and disgust spreading to V5/MT+ in the dynamic condition. Thus, dynamic face characteristics might result in an enhanced visual motion analysis in V5/MT+ (Dumoulin et al., 2000) possibly induced by more natural and complex stimulus properties, hence, recruiting more attentional resources and resulting in stronger and more widespread activation patterns. The possible recruitment of more attentional resources could be underlined by the increased arousal rates for both disgust and happiness compared to neutrality which were revealed during the post-fMRI-rating for the emotional conditions.

The STS area has been associated with the processing of biological motion of changeable aspects in studies of, e.g., body and face perception (Allison et al., 2000; Grossman and Blake, 2002; Haxby et al., 2000; Pelphrey et al., 2003; Puce et al., 1998) and with the perception of dynamic facial emotions of

anger and fear, indicating an interaction of emotion and motion (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004; Wicker et al., 2003). Confirming our hypothesis, we found enhanced STS area activation patterns for the perception of dynamic disgusted (STS area) and happy (V5/MT+ and STS area) facial expressions. Biological motion aspects of stimuli (e.g., gaze, muscular changes of the face) apparently conveyed a higher complexity of social cues, which are important for adequate social communication, and, hence, probably evoked stronger neural activation patterns.

3.4. Amygdala

As study participants watched the stimulus material for the first time, dynamic faces conveyed strong salience. In the present study we found amygdala activation only for dynamic disgust perception but not for the perception of happy dynamic stimuli.

It has been a long ongoing debate whether the amygdala is exclusively related to negative salient stimuli. On the one hand, emotional face perception of potentially salient and negative facial stimuli was reported to be linked to amygdala activation (Anderson et al., 2003; Fitzgerald et al., 2004; LaBar et al., 2003; Phillips et al., 1998; Williams et al., 2005), which was even enhanced when dynamic negative facial expressions were presented (e.g. fear and anger; Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). On the other hand, amygdala activation has also been reported for the perception of positive emotional facial expressions (Canli et al., 2002; Costafreda et al., 2008; Phan et al., 2002; Yang et al., 2002). According to a meta-analysis of 385 imaging studies published by Costafreda et al. (2008) the probability to reveal amygdala activation is higher in perception of fear and disgust compared to happiness. They argued that amygdala activation might be related to arousal instead of valence or to stimulus ambiguity as also suggested by Davis and Whalen (2001). According to the latter argument, it might be possible that happy stimuli appeared to be less ambiguous to the participants of the present study than the faces of disgust because humans have more experience with happy compared to disgusted faces in everyday social interactions and seemed to be processed faster than negative stimuli (Leppanen and Hietanen, 2004). This data might explain why the amygdala was only activated for stimuli of disgust in the present study.

3.5. Frontal regions

Inferior frontal regions including Broca's area have traditionally been associated with motor speech production and semantic interpretation, but also – among other regions – with the human "mirror neuron system" (MNS; for review, see Rizzolatti et al. (2001)). In humans, the MNS has been shown to be activated during passive observation of mouth, hand or foot movements (Buccino et al., 2001; Iacoboni et al., 1999) and during passive observation of facial emotional expressions (Hennenlotter et al., 2005; Lee et al., 2006; Leslie et al., 2004; Sato et al., 2004). Furthermore, the visual representation of facial affect has been shown to be related to its internal motor representations (Hennenlotter et al., 2005). Thus, the present finding of inferior frontal cortex and premotor area activation

might reflect "mirroring" and/or activating internal representations of the observed action without actual execution (Iacoboni et al., 1999; Rizzolatti et al., 2002). The lack of activation in inferior frontal regions for happy faces might be explained by a faster and more automatic processing (Leppanen and Hietanen, 2004). However, we only found supplementary motor area (SMA) activation for happiness, which has also been associated with the MNS (Lee et al., 2006; Leslie et al., 2004).

The present study showed activation in ventromedial/ orbitofrontal regions during the processing of happy and disgusted facial expressions which was enhanced for dynamic compared to static stimuli (see Fig. 3). On the one hand, OFC activation has been shown to be related to reward processing and social reward for happy facial expressions (Gorno-Tempini et al., 2001; Kim et al., 2003; O'Doherty et al., 2003). On the other hand, however, our data indicate that the OFC region might not be exclusively recruited for positively valenced emotional facial expressions and social reward processing. The OFC might also be associated with the monitoring, reflection on and assessment of internal emotional experience and emotional regulation as suggested in a study by Garrett and Maddock (2006) examining the perception and processing of aversive stimuli. Furthermore, a previous fMRI study has shown that the OFC was activated during the processing of both pleasant and unpleasant tastes (O'Doherty et al., 2001). Therefore, as we revealed OFC activation for both disgust and happiness, we assume that the OFC is involved in emotion and evaluation processing of positive and negative stimuli.

3.6. Summary and integration of data with current emotion perception models

Summarizing, the present fMRI data obtained during the perception of dynamic facial expressions corroborate Adolphs' (2002) model with a few exceptions. Activation of the thalamus, brain stem regions, and hypothalamus did not show up. The latter regions have predominantly been ascribed to the fast early perceptual processing within the first 120 to 300 ms after stimulus presentation. Due to the fast and transient activation of those regions, they might have been
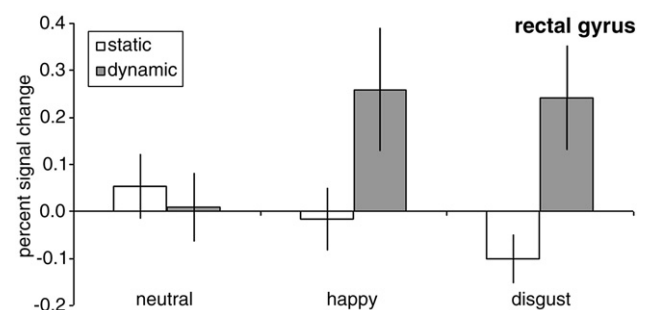

Fig. 3 – Percent signal change graph of the ROI left rectal gyrus for all emotional categories and modalities were derived from the Marsbar toolbox (http://marsbar.sourceforge.net). Bright bars indicate the static stimulus condition (±1 standard error of mean (SEM)), grey bars show the dynamic stimulus condition (±1 SEM).

involved in emotional face processing, but fMRI might not have been sensible enough to detect neural activation (Im, 2007). The revealed and discussed brain regions were, hence, mainly in line with the brain areas suggested to be part of the emotion perception network by Adolphs (2002) and the face perception model reported by Haxby et al. (2000).

3.7. Why did we not find insula activation during the processing of disgust facial expressions?

In contrast to our working hypothesis, we did not find insula activation during disgust perception of facial expressions. As far as we know there is only one fMRI study focusing on the rating of valence, arousal and dominance of fearful and disgusting scenes (IAPS pictures), which did not report insula activation, but amygdala, medial prefrontal and fusiform gyrus activation during the disgust condition (Stark et al., 2003). A major detail where our study differs from other studies was the presentation duration of the emotional expression. In some studies reporting insula activation during perception of disgusted facial expressions stimuli were presented for 2.5 s, 3 s or even longer (Gorno-Tempini et al., 2001; Phillips et al., 1997, 1998; Sprengelmeyer et al., 1998; Williams et al., 2005). A presentation of 1.5 s in the present study was presumably too short to capture the necessary resources for activation of the insula and a parasympathetic reaction which takes more time than, e.g., activation of amygdala via a fast subcortical emotion perception route (LeDoux, 1996) and a following fast sympathetic fear response (Rozin and Fallon, 1987; Williams et al., 2005).

A further reason for the lack of insula activation might be that participants were simply mirroring the shown expressions without directly "feeling" disgust. Leslie et al. (2004) reported that participants passively watched smiling and frowning faces and showed stronger right lateralized inferior frontal activation. They hypothesized that this activation was related to emotion processing and mirroring the perceived emotional stimuli. Since inferior frontal activation was confirmed for disgust perception in the present study, the authors speculate that participants rather mirrored the negative expressions instead of "feeling" disgust per se. This aspect supports the above-mentioned line of argumentation of the mirror neuron system and the inferior frontal gyrus activation.

3.8. Are dynamic facial expression stimuli more valid than static stimuli?

We will discuss the finding of a larger and more widespread network of brain areas involved in emotion perception for dynamic compared to static stimuli in relation to three major aspects:

First, on a feature-based level, static and moving faces displaying an emotional expression convey both specific structural features (eyes, mouth, nose, hair etc.), whereas dynamic face stimuli additionally mediate very complex and rapid changing temporal cues of information. Thus, faces switching from a neutral to a happy expression display a change of facial muscles in a certain temporal sequence. Our participants, therefore, were able to relate the different

changing features to one another, which was suggested to specifically improve the three-dimensional perception of faces (Knight and Johnston, 1997), to enhance the perception of emotional expressions (Ambadar et al., 2005), to facilitate appropriate emotion recognition, and to reflect social interactions in a more natural way (Bassili, 1979; Berry, 1990; Knight and Johnston, 1997; LaBar et al., 2003; Sato et al., 2004). Better recognition accuracy of dynamic compared to static stimuli have also been confirmed in autism (Gepner et al., 2001), mentally retarded children (Harwood et al., 1999) and agnostic patients (Humphreys et al., 1993) on the behavioral level, and have been linked to brain activation in neuroimaging studies (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004).

Second, dynamic facial expressions were described to enrich emotional perception of facial expressions (Biele and Grabowska, 2006) and to capture the liveliness and true form of facial expressions because they typically occur in everyday life (Harwood et al., 1999) and, hence, appear more natural and more ecologically valid. Indeed, we do not face static faces when we socially interact with other people. We have a long learning history of analyzing and interpreting facial emotional expressions "in motion" from childhood on which results in a large amount of experience and memory of dynamic faces.

Third, post hoc evaluation of dynamic and static stimuli revealed increased arousal rates for the dynamic modality per se.

These three aspects are largely corroborated by the present neuroimaging and behavioral findings: The more widespread activation pattern of dynamic compared to static emotional faces might be explained by (1) a higher complexity of stimuli, (2) a higher authenticity and appropriateness of dynamic faces, and (3) higher arousal rates. The present data furthermore showed a significantly higher accuracy rate for disgust for dynamic in contrast to static facial expressions (see also Biele and Grabowska, 2006; Simons et al., 1999). These data were also substantiated by an evaluation study of the dynamic stimulus material conducted with 30 women including 5 different emotion categories (neutral, happiness, disgust, fear, and anger), which revealed accuracy rates of 93, 98 and 94% of neutral, happy and disgusted dynamic facial expressions, respectively. Therefore, we suggest that the higher complexity of dynamic facial expressions might be reflected by more widespread activation patterns on the one hand. On the other hand, it might be easier to perceive and correctly recognize a dynamic face – as reflected by a higher recognition accuracy of dynamic stimuli – because we are more experienced in dynamic face processing. Furthermore, dynamic facial expressions might simply appear more interesting and exciting compared to static expressions. In conclusion, dynamic facial expressions seem to be more ecologically valid and, thus, more natural stimuli should be used in future studies addressing emotion processing.

3.9. Why did static emotional material hardly produce BOLD activation differences?

In the present investigation perceptual processing of static emotional stimuli hardly produced reliable significant BOLD activation despite a lower significance threshold. This result additionally supports the above-mentioned assumption that

dynamic stimuli provide a more ecologically valid approach for triggering brain responses related to emotional face processing. There might be different reasons for this finding.

Because of the different stimulus properties of (1) the videos including the turn to the front and (2) the static facial expressions including solely front view of the face one could expect different activation patterns because the dynamic stimuli were all in all presented longer than the static stimuli. However, there are three aspects why an overlay of neural activation of the turn onto the emotional processing was probably cancelled out:

First, exclusively the modeled hitpoints of the apex of the emotional expressions and their duration till the end of the video were included in the analysis. Second, dynamic emotional and neutral stimuli followed the same structure in all categories, and third, both static and dynamic stimuli were contrasted to each other only within their modality before entering those emotion effects in a further interaction analysis. Therefore, the differing duration of stimulus presentation were not assumed to matter for further analysis steps.

Static stimuli might not have equivalent salience compared to dynamic stimuli because they do not convey rapidly changing cues of information. Consequently, as discussed above, static faces are not perceived as natural and powerful as dynamic facial stimuli resulting in lower recognition accuracy rates. However, this line of argumentation might not be the most convincing one because many other different emotion perception studies using, e.g., static facial expressions (Ekman and Friesen, 1976), have discussed a network of brain regions during emotion perception (for review, see Adolphs (2002); Phan et al. (2002)).

Another argument could be that generally diminished arousal rates for static stimuli might also account for diminished cortical and subcortical activations compared to the processing of dynamic emotional faces because motion per se captures attention. Therefore, participants' attention might not have been as consistently captured by static stimuli as by dynamic ones. As we did not include a behavioral response because we wanted to avoid cognitive control on our emotion perception design (see Experimental procedures section and Costafreda et al. (2008); Lange et al. (2003)), we were not able to control directly for participant's attention within the emotional perception blocks. This is a limitation of the study. In future studies, it would be interesting to discriminate attention effects by adding a simple task with attentional load in order to be better able to isolate effects of motion on emotion.

Furthermore, the perception of static facial expressions might result in a higher interindividual-variance and/or a higher intertrial-variability compared to dynamic stimuli. Thus BOLD activation might not have reached statistical significance as reliably as dynamic stimuli resulting in less widespread activation patterns.

3.10. Limitations of the study

One of the limitations of the study refers to the 'open' task instruction. Participants simply watched the emotional stimuli passively without having to respond according to a task.

Thus, we do not exactly know whether all participants engaged in the same processes while watching the stimuli. However, we chose this task to avoid an influence of cognitive processes (top-down processes) on emotion perception because previous studies have reported different neural activation patterns for passive versus active task instructions (see, e.g., Costafreda et al., 2008; Lange et al., 2003). Our goal was to study emotion perception and not to study the induction of feelings or cognitive evaluation of emotional static and dynamic stimuli.

Therefore, it would be interesting in future studies to compare the influence of different task instructions on neural activation patterns, like, e.g. an explicit emotional rating task, an implicit gender discrimination task, an empathizing task and a passively, attentively viewing task for this new dynamic and static stimulus database.

4. Conclusion

The results of the present study indicate that dynamic face stimuli result in more pronounced and distributed activation patterns when compared to static faces. This finding is interpreted in terms of higher ecological validity of the dynamic face stimuli facilitating the perception of emotional facial expressions, and recruiting more widespread emotion-specific neuronal networks possibly due to a higher complexity of stimuli and parallel processing of information. Except for two studies focusing on the perception of disgust-inducing film clips (Stark et al., 2005) and videos showing people smelling disgusting, pleasant or neutral odors (Wicker et al., 2003), to our knowledge, there has been no studies reporting an enhancement of activation for dynamic compared to static facial expressions of disgust-inducing network activation, e.g., in the amygdala, fusiform face area, the superior temporal sulcus area, and lateral inferior frontal areas as discussed in the present investigation.

In our view, the research of emotion perception is "in motion". Humans are experts for the processing of authentic moving faces in social interactions. This is one of the main reasons why we suggest to examine face and emotion processing considering authentic dynamic stimuli to more appropriately quantify and qualify the respective both normal and impaired brain physiological processing (Gepner et al., 2001; Harwood et al., 1999; Humphreys et al., 1993).

5. Experimental procedures

5.1. Participants

The fMRI study group consisted of 16 female adults between 19 and 27 years (21.6±2.3 years) from Bremen University campus. We only included female participants in order to avoid gender effects in neural activation patterns and emotion perception which have been previously reported in neuroimaging studies of emotion for males and females (for review, see Wager et al. (2003)). It was stated that women show stronger activation during emotional processing tasks compared to men (Wager et al., 2003). All participants were right-handed according to a

modified version of the Edinburgh Handedness Inventory Questionnaire (Laterality Quotient: 92.3% SD 9.7, range 69.2–100%; Oldfield, 1971), did not report any history of neurological or psychiatric illness, and were under no current medication affecting the central nervous system. All participants were native German speakers with 14 to 18 years of education (15.1±1.5 years) and had normal or corrected to normal visual acuity. The participants gave informed and written consent to participate in the fMRI-experiment. The study protocol was designed and performed according to the Helsinki Declaration (1964) and was approved by the local ethics committee of the University of Bremen.

5.2. Evaluation study of dynamic facial expression material

We used a new stimulus set of dynamic emotional expressions (Fig. 4A) and therefore, we wanted to ensure that emotional valences like, e.g., disgust were actually perceived as disgust even among a choice of other negative stimuli (here: fear and anger). Consequently, we recruited a sample of 30 psychiatrically and neurologically healthy female adults (mean age 22.7±2.9 years, education 15.4±1.9 years, Handedness: Lateralization Quotient [LQ] 95.3±15.5) for a behavioral evaluation study of the new dynamic stimulus material. Again, we chose only female participants in order to avoid gender effects of emotion perception (for review, see Wager et al. (2003)). Participants gave informed and written consent in the study.

Participants watched 40 female actresses. As female and male emotional faces are perceived differently by men and women (Marinkovic and Halgren, 1998; Orozco and Ehlers, 1998), we only presented female faces. Orozco and Ehlers (1998), for example, have reported faster reaction times of female participants to male happy than to female happy faces and in an EEG study on emotion perception by Marinkovic and Halgren (1998), male participants showed higher amplitudes for female happy faces than to male happy faces. To avoid these differences we decided to only present female facial expressions. Dynamic facial expressions of

happiness, neutrality, disgust, anger, and fear (hence 40 per emotion, altogether 200 Stimuli; see also Fig. 4A for stimulus description and below for further details of stimulus construction) were presented on a black background in a pseudo-randomized non-stationary probabilistic sequence (Friston et al., 1999c). Participants were asked to rate the videos according to arousal (on a scale from 0 [no arousal] to 10 [very high arousal]) and valence (happiness, neutral, disgust, fear, and anger, 40 of each valence). The setting was comparable to the post-fMRI-rating of the dynamic stimuli (see below for more detailed description of stimuli and the experimental setup).

5.3. Experimental design

A set of emotional videos and video screen captures showing different facial expressions (see Fig. 4) was applied for the fMRI study. The stimuli were depicted from a stimulus data base of 40 female and 40 male non-professional actors displaying each of eight different emotional facial expressions (happiness (smiling and laughing), surprise, enjoying, fear, anger, sadness, and disgust) and neutral expressions. Actors were placed in front of a video camera (70 cm distance between face and camera, black background, darkened room with virtually equally held illumination). Emotional expressions of actresses were triggered by a mood induction strategy (e.g. for disgust: "imagine, you come home after two weeks of vacation but you forgot to take out the biowaste container" or happy: "imagine you meet someone unexpectedly on the street who you really like and give him a smile because you are happy to see him").

For the purposes of the present study, only female dynamic and static emotional face stimuli ($N=40$; see above for detailed explanation of gender differences) displaying positive (happiness), negative (disgust), and neutral expressions were used. We chose happiness and disgust in order to allow for the distinguished analysis of emotion-specific processing instead of pure arousal processing on the neural level. Each video followed the same type of scenario (see below and Fig. 4A, for illustration).
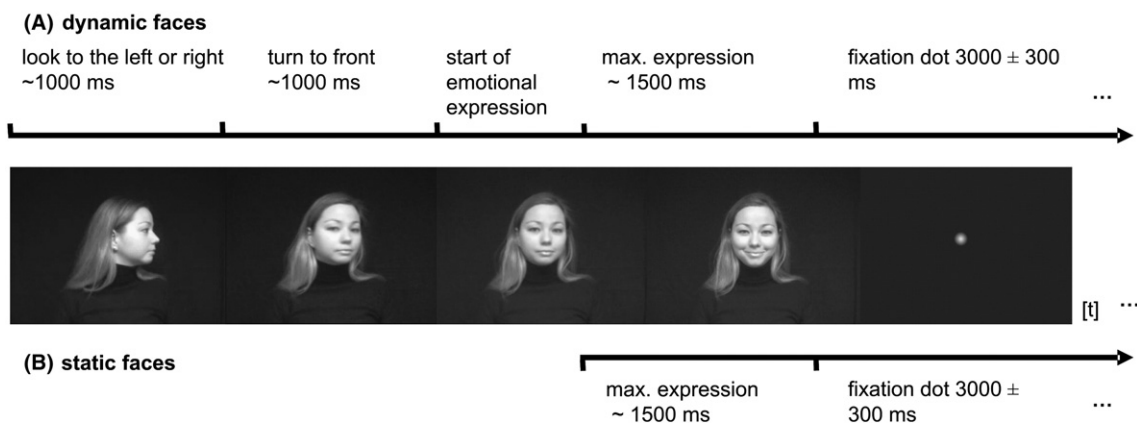

Fig. 4 – Example for trial sequences for dynamic (A, upper row) and static faces (B, lower row). (A) The actress looked to the right (left) with an angle of 90° to the camera (black background), turned towards the camera after approximately one second and started expressing a neutral, happy or disgusted face as soon as she faced the camera frontally. (B) The maximum emotional expression was captured from the videos for the static modality.

Videos were recorded in mpg2-format and then converted to mpg1-format (PAL: 25 frames/s, 352×576, ratio 4:3; TMPGEnc Plus©, version 2.510.49.157). Static stimuli were captured from the videos at the maximum (max.) of each frontally presented neutral or emotional expression saved in jpg-format, 96×96 dpi resolution, 24 bitdepth; Paint Shop Pro©, version 5.01, Jasc software, Inc., Fig. 4B). Videos and static video frame captures were presented using Presentation®-software (Neurobehavioral Systems, https://nbs.neuro-bs.com) via a digital projector on a mirror in the scanner tube.

The presentation duration of the videos and static facial expressions and the timing of the videos were determined by applying a hitpoint analysis in which the time points of each video of the beginning of the turn, the frontal position, the first hint of emotion, the first subjective recognition of the emotion, the apex of emotional expression and the entire duration of the video were assigned. Hitpoint analyses were conducted by the first author of the present paper and by two independent female students. Hitpoint raters determined the first subjective recognition of happiness and disgust and their maximum. Correlating the data of all raters (Pearson Correlation) showed a significant correlation (all $p < .001$) among raters, which supported the reliability of the applied hitpoints for the present two studies.

The results of this hitpoint analysis confirmed an average video-length of 3.7 s (for neutrality, happiness, and disgust) and showed an average duration of the maximum of emotional expression (for neutral, average time of the frontal position of the face till the end of the video was chosen) of 1499 ms. Therefore, the presentation time for the static facial expressions was set to 1500 ms in order to allow for a comparable fMRI data modeling for both static and dynamic stimulus modalities. Facial stimuli were followed by a fixation dot (3000±300 ms), thus resulting in an average trial duration of about 4.5 s for the static and about 6.7 s for the dynamic faces (for illustration see Figs. 4A, B).

Static and dynamic stimuli (120 stimuli for each modality: 40 disgusted, 40 happy and 40 neutral expressions, respectively) were presented in two separate and counterbalanced runs during one fMRI-session. Each run consisted of 4 blocks (average duration of all four blocks together: 18 min for static and 23 min for dynamic faces) which were separated by 2 min sequences of stimulus–response-compatibility tasks and a 15 s resting period in order to ensure an appropriate vigilance level. Stimuli were presented in a pseudo-randomized non-stationary probabilistic sequential order (Friston et al., 1999c), based on the assumption that the effect of emotional stimuli persist up to half a minute or longer after stimulation (Garrett and Maddock, 2001). This procedure provides an appropriate compromise between event-related and block design, thus avoiding habituation effects usually appearing in emotion perception studies with block designs (Breiter et al., 1996) especially in subcortical, emotion-sensitive areas like the amygdala. Between runs, participants had between 3 to 5 min to rest.

Participants were asked to fixate a dot in the center of the screen, to watch the videos and the static video frame captures passively (= no button press needed to avoid top-down processes) and carefully, and to 'be open' to the perceived expressions. Thus, we wanted to study emotion

perception, but not the 'induction or feeling of emotions' or 'cognitive evaluation of emotions' per se. After the fMRI scanning session, participants rated the presented dynamic and static stimuli according to arousal (on a scale from 0 [no arousal] to 10 [very high arousal]) and valence (happiness, neutrality, disgust).

5.4.   FMRI data acquisition and analyses

Functional (T2*-weighted gradient echo-planar imaging, EPI, sequence, 44 contiguous slices aligned to the AC–PC line, slice thickness 3 mm, no gap, interleaved acquisition, TR=2500 ms, TE=30 ms, flip angle 90°, 64×64 matrix, FOV 192×192) and structural (MPRAGE, T1-weighted sequence, 160 slices, TR 2300 ms, TE 4.38 ms, flip angle=8°, TI 900 ms, FOV 256×256, 1 mm³ voxel, saggital orientation) MRI data were recorded on a 3-T SIEMENS Allegra System (Siemens, Erlangen, Germany).

FMRI data analyses were performed using the statistical parametric mapping software SPM2 (Wellcome Department of Cognitive Neurology, London, UK, http://www.fil.ion.ucl.ac.uk/spm/). Parameter estimates for percent signal change were calculated using the Marsbar toolbox (http://marsbar.sourceforge.net). After discarding the first two volumes of each run to allow for magnetic saturation, all functional data were slice-time corrected, realigned and unwarped to the 10th volume, spatially normalized (bounding box, template: 90:90, −126:90, −72:108, trilinear interpolation) to the Montreal Neurological Institute (MNI) stereotactic EPI template and resampled to 2×2×2 mm voxel size. Thereafter, data were smoothed with a Gaussian Kernel of 8 mm (full width half maximum, FWHM) in order to increase the signal-to-noise (SNR) ratio of the data and to compensate for anatomical variability between participants (Glascher et al., 2004; Sato et al., 2004). To model the data at first level, trial related stimulus durations were convolved with the canonical hemodynamic response function (Della-Maggiore et al., 2002; Friston et al., 1999a,b) and locked to the respective stimulus onsets.

Data were corrected for intrinsic autocorrelation (AR (1)) and high-pass filtered (128 Hz) to remove low frequency signal drifts. The design matrix comprised 8 regressors for the embedded inter-block stimulus–response-compatibility task, which was no further subject of the present study, 3 regressors for the emotional facial expression categories (plus 3 regressors, exclusively for the videos, modeling the turn of the actress' head until the first emotional expression could be recognized), 1 regressor covering dummy variables (instruction text and resting epochs), 1 regressor for errors and misses during the embedded stimulus–response-compatibility task, and 6 realignment parameters (x, y, z, and the three rotation angles, as regressors of no interest in order to minimize false-positive activations due to task-related motion of the subjects, see also Johnstone et al., 2006). Second-level whole-brain random effects analyses (Holmes and Friston, 1998) were performed by calculating a t-statistic for predetermined condition effects at each voxel for each participant and run and producing a statistical image for the contrasts disgust > neutrality, happiness > neutrality, and vice versa, separately for both static and dynamic stimulus modalities. These individual contrast images were used to identify the main emotion effects by means of a one sample t-test. In line with

previous fMRI studies examining emotional face perception (Kilts et al., 2003; Sato et al., 2004), we set the significance level to $p < .001$ (unless reported differently), uncorrected, and applied a spatial threshold of $k = 20$ voxels. To detect modality-specific differences between the dynamic and static face perception processing, interaction analyses (one-way ANOVA) for stimulus modality (static vs. dynamic) were calculated including the respective contrast images as defined above, e.g. ([dynamic_disgust > dynamic_neutral] versus [static_disgust > static_neutral]) and ([dynamic_happy > dynamic_neutral] versus [static_happy > static_neutral]) using the same significance threshold of $p < .001$ uncorrected, with a spatial threshold of $k = 20$ voxels (see above).

Functional regions of interest (ROIs) were determined on the basis of significant cluster peak activations revealed by the interaction analysis ($p < .001$, $k = 20$, uncorrected). For each ROI, stimulus modality, and emotional category, percent signal change values have been calculated. For percent signal change values of the amygdala, a spatial ROI mask for this region was determined using the wfu-pickatlas toolbox (Brodmann areas, 3-D, dilatation 0, http://www.fmri.wfubmc.edu/download.htm). MNI-coordinates of significant voxel clusters from MNI (Montreal Neurological Institute) were converted to Talairach space (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach, Talairach and Tournoux, 1988) using a Matlab® tool (mni2tal.m, http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach), and the corresponding anatomical regions were determined using the Talairach Daemon Client software (http://ric.uthscsa.edu/projects/talairachdaemon.html).

Acknowledgments

REFERENCES

Adolphs, R., 2002. Recognizing emotion from facial expressions: psychological and neurological mechanisms. Behav. Cogn. Neurosci. Rev. 1, 21–61.

Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4, 267–278.

Ambadar, Z., Schooler, J.W., Cohn, J.F., 2005. Deciphering the enigmatic face: the importance of facial dynamics in interpreting subtle facial expressions. Psychol. Sci. 16, 403–410.

Anderson, A.K., Christoff, K., Panitz, D., De Rosa, E., Gabrieli, J.D., 2003. Neural correlates of the automatic processing of threat facial signals. J. Neurosci. 23, 5627–5633.

Bassili, J.N., 1979. Emotion recognition: the role of facial movement and the relative importance of upper and lower areas of the face. J. Pers. Soc. Psychol. 37, 2049–2058.

Berry, D.S., 1990. What can a moving face tell us? J. Pers. Soc. Psychol. 58, 1004–1014.

Biele, C., Grabowska, A., 2006. Sex differences in perception of emotion intensity in dynamic and static facial expressions. Exp. Brain Res. 171, 1–6.

Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S.E., Rosen, B.R., 1996. Response and habituation of the human amygdala during visual processing of facial expression. Neuron. 17, 875–887.

Bruce, V., Young, A., 1986. Understanding face recognition. Br. J. Psychol. 77, 305–327.

Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., Freund, H.J., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur. J. Neurosci. 13, 400–404.

Canli, T., Sivers, H., Whitfield, S.L., Gotlib, I.H., Gabrieli, J.D., 2002. Amygdala response to happy faces as a function to extraversion. Science 296, 2191.

Costafreda, S.G., Brammer, M.J., David, A.S., Fu, C.H.Y., 2008. Predictors of amygdala activation during the processing of emotional stimuli: a meta-analysis of 385 PET and fMRI studies. Brain Res. Rev. 58, 57–70.

Davidson, R.J., Irwin, W., 1999. The functional neuroanatomy of emotion and affective style. Trends Cogn. Sci. 3, 11–21.

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

Della-Maggiore, V., Chau, W., Peres-Neto, P.R., McIntosh, A.R., 2002. An empirical comparison of SPM preprocessing parameters to the analysis of fMRI data. Neuroimage 17, 19–28.

Dumoulin, S.O., Bittar, R.G., Kabani, N.J., Baker Jr., C.L., Le Goualher, G., Bruce Pike, G., Evans, A.C., 2000. A new anatomical landmark for reliable identification of human area V5/MT: a quantitative analysis of sulcal patterning. Cereb. Cortex 10, 454–463.

Ekman, P., Friesen, W.V., 1976. Pictures of Facial Affect, Vol., Consulting Psychologists. Palo Alto.

Fitzgerald, D.A., Posse, S., Moore, G.J., Tancer, M.E., Nathan, P.J., Phan, K.L., 2004. Neural correlates of internally-generated disgust via autobiographical recall: a functional magnetic resonance imaging investigation. Neurosci. Lett. 370, 91–96.

Friston, K.J., Holmes, A.P., Price, C.J., Buchel, C., Worsley, K.J., 1999a. Multisubject fMRI studies and conjunction analyses. Neuroimage 10, 385–396.

Friston, K.J., Holmes, A.P., Worsley, K.J., 1999b. How many subjects constitute a study? Neuroimage 10, 1–5.

Friston, K.J., Zarahn, E., Josephs, O., Henson, R.N., Dale, A.M., 1999c. Stochastic designs in event-related fMRI. Neuroimage 10, 607–619.

Garrett, A.S., Maddock, R.J., 2001. Time course of the subjective emotional response to aversive pictures: relevance to fMRI studies. Psychiatry Res. 108, 39–48.

Garrett, A.S., Maddock, R.J., 2006. Separating subjective emotion from the perception of emotion-inducing stimuli: an fMRI study. Neuroimage 33, 263–274.

Gepner, B., Deruelle, C., Grynfeltt, S., 2001. Motion and emotion: a novel approach to the study of face processing by young autistic children. J. Autism Dev. Disord. 31, 37–45.

Glascher, J., Tuscher, O., Weiller, C., Buchel, C., 2004. Elevated responses to constant facial emotions in different faces in the human amygdala: an fMRI study of facial identity and expression. BMC Neurosci. 5, 45.

Gorno-Tempini, M.L., Pradelli, S., Serafini, M., Pagnoni, G., Baraldi, P., Porro, C., Nicoletti, R., Umita, C., Nichelli, P., 2001. Explicit and incidental facial expression processing: an fMRI study. Neuroimage 14, 465–473.

Grill-Spector, K., Knouf, N., Kanwisher, N., 2004. The fusiform face area subserves face perception, not generic within-category identification. Nat. Neurosci. 7, 555–562.

Grossman, E.D., Blake, R., 2002. Brain areas active during visual perception of biological motion. Neuron 35, 1167–1175.

Halgren, E., Dale, A.M., Sereno, M.I., Tootell, R.B.H., Marinkovic, K., Rosen, B.R., 1999. Location of human face-selective cortex with respect to retinotopic areas. Hum. Brain Mapp. 7, 29–37.

Harwood, N.K., Hall, L.J., Shinkfield, A.J., 1999. Recognition of facial emotional expressions from moving and static displays by individuals with mental retardation. Am. J. Ment. Retard. 104, 270–278.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cogn. Sci. 4, 223–233.

Hennenlotter, A., Schroeder, U., Erhard, P., Castrop, F., Haslinger, B., Stoecker, D., Lange, K.W., Ceballos-Baumann, A.O., 2005. A common neural basis for receptive and expressive communication of pleasant facial affect. Neuroimage 26, 581–591.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat. Neurosci. 3, 80–84.

Holmes, A.P., Friston, K.J., 1998. Generalisability, Random Effects & Population Inference. Wellcome Department of Cognitive Neurology, Institute of Neurology London, UK.

Humphreys, G.W., Donnelly, N., Riddoch, M.J., 1993. Expression is computed separately from facial identity, and it is computed separately for moving and static faces: neuropsychological evidence. Neuropsychologia 31, 173–181.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 2526–2528.

Im, C.H., 2007. Dealing with mismatched fMRI activations in fMRI constrained EEG cortical source imaging: a simulation study assuming various mismatch types. Med. Biol. Eng. Comput. 45, 79–90.

Johnstone, T., Ores Walsh, K.S., Greischar, L.L., Alexander, A.L., Fox, A.S., Davidson, R.J., Oakes, T.R., 2006. Motion correction and the use of motion covariates in multiple-subject fMRI analysis. Hum. Brain Mapp. 27, 779–788.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.

Kilts, C.D., Egan, G., Gideon, D.A., Ely, T.D., Hoffman, J.M., 2003. Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. Neuroimage 18, 156–168.

Kim, H., Somerville, L.H., Johnstone, T., Alexander, A.L., Whalen, P.J., 2003. Inverse amygdala and medial prefrontal cortex responses to surprised faces. Neuroreport 14, 2317–2322.

Knight, B., Johnston, A., 1997. The role of movement in face recognition. Vis. Cogn. 4, 265–273.

Kosslyn, S.M., Shin, L.M., Thompson, W.L., McNally, R.J., Rauch, S.L., Pitman, R.K., Alpert, N.M., 1996. Neural effects of visualizing and perceiving aversive stimuli: a PET investigation. Neuroreport 7, 1569–1576.

Krumhuber, E., Kappas, A., 2005. Moving smiles: the role of dynamic components for the perception of the genuineness of smiles. J. Nonverbal Behav. 29, 2–24.

LaBar, K.S., Crupain, M.J., Voyvodic, J.T., McCarthy, G., 2003. Dynamic perception of facial affect and identity in the human brain. Cereb. Cortex 13, 1023–1033.

Lane, R.D., Fink, G.R., Chau, P.M., Dolan, R.J., 1997. Neural activation during selective attention to subjective emotional responses. Neuroreport 8, 3969–3972.

Lange, K., Williams, L.M., Young, A.W., Bullmore, E.T., Brammer, M.J., Williams, S.C., Gray, J.A., Phillips, M.L., 2003. Task instructions modulate neural responses to fearful facial expressions. Biol. Psychiatry 53, 226–232.

LeDoux, J., 1996. The Emotional Brain: The Mysterious Underpinnings of Emotional Life. Simon & Schuster, New York.

Lee, T.W., Josephs, O., Dolan, R.J., Critchley, H.D., 2006. Imitating expressions: emotion-specific neural substrates in facial mimicry. Soc. Cogn. Affect Neurosci. 1, 122–135.

Leppanen, J.M., Hietanen, J.K., 2004. Positive facial expressions are recognized faster than negative facial expressions, but why? Psychol. Res. 69, 22–29.

Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. Neuroimage 21, 601–607.

Marinkovic, K., Halgren, E., 1998. Human brain potentials related to the emotional expression, repetition, and gender of faces. Psychobiology 26, 348–356.

Murphy, F.C., Nimmo-Smith, I., Lawrence, A.D., 2003. Functional neuroanatomy of emotions: a meta-analysis. Cogn. Affect Behav. Neurosci. 3, 207–233.

Narumoto, J., Okada, T., Sadato, N., Fukui, K., Yonekura, Y., 2001. Attention to emotion modulates fMRI activity in human right superior temporal sulcus. Brain Res. Cogn. Brain Res. 12, 225–231.

O'Doherty, J., Rolls, E.T., Francis, S., Bowtell, R., McGlone, F., 2001. Representation of pleasant and aversive taste in the human brain. J. Neurophysiol. 85, 1315–1321.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., Dolan, R.J., 2003. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. Neuropsychologia 41, 147–155.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.

Orozco, S., Ehlers, C.L., 1998. Gender differences in electrophysiological responses to facial stimuli. Biol. Psychiatry 44, 281–289.

Pelphrey, K.A., Singerman, J.D., Allison, T., McCarthy, G., 2003. Brain activation evoked by perception of gaze shifts: the influence of context. Neuropsychologia 41, 156–170.

Pessoa, L., McKenna, M., Gutierrez, E., Ungerleider, L.G., 2002. Neural processing of emotional faces requires attention. Proc. Natl. Acad. Sci. U. S. A. 99, 11458–11463.

Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. Neuroimage 16, 331–348.

Phillips, M.L., Young, A.W., Senior, C., Brammer, M., Andrew, C., Calder, A.J., Bullmore, E.T., Perrett, D.I., Rowland, D., Williams, S.C., Gray, J.A., David, A.S., 1997. A specific neural substrate for perceiving facial expressions of disgust. Nature 389, 495–498.

Phillips, M.L., Young, A.W., Scott, S.K., Calder, A.J., Andrew, C., Giampietro, V., Williams, S.C., Bullmore, E.T., Brammer, M., Gray, J.A., 1998. Neural responses to facial and vocal expressions of fear and disgust. Proc. R. Soc. Lond., B. Biol. Sci. 265, 1809–1817.

Puce, A., Allison, T., Bentin, S., Gore, J.C., McCarthy, G., 1998. Temporal cortex activation in humans viewing eye and mouth movements. J. Neurosci. 18, 2188–2199.

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2, 661–670.

Rizzolatti, G., Fogassi, L., Gallese, V., 2002. Motor and cognitive functions of the ventral premotor cortex. Curr. Opin. Neurobiol. 12, 149–154.

Rozin, P., Fallon, A.E., 1987. A perspective on disgust. Psychol. Rev. 94, 23–41.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., Matsumura, M., 2004. Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. Brain Res. Cogn. Brain Res. 20, 81–91.

Schienle, A., Stark, R., Walter, B., Blecker, C., Ott, U., Kirsch, P., Sammer, G., Vaitl, D., 2002. The insula is not specifically involved in disgust processing: an fMRI study. Neuroreport 13, 2023–2026.

Simons, R.F., Detenber, B.H., Roedema, T.M., Reiss, J.E., 1999. Emotion processing in three systems: the medium and the message. Psychophysiology 36, 619–627.

Sprengelmeyer, R., Rausch, M., Eysel, U.T., Przuntek, H., 1998. Neural structures associated with recognition of facial expressions of basic emotions. Proc. R. Soc. Lond., B. Biol. Sci. 265, 1927–1931.

Stark, R., Schienle, A., Walter, B., Kirsch, P., Sammer, G., Ott, U., Blecker, C., Vaitl, D., 2003. Hemodynamic responses to fear and disgust-inducing pictures: an fMRI study. Int. J. Psychophysiol. 50, 225–234.

Stark, R., Schienle, A., Girod, C., Walter, B., Kirsch, P., Blecker, C., Ott, U., Schafer, A., Sammer, G., Zimmermann, M., Vaitl, D., 2005. Erotic and disgust-inducing pictures—differences in the hemodynamic responses of the brain. Biol. Psychol. 70, 19–29.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme, Stuttgart.

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. Neuron. 30, 829–841.

Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R. J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. Nat. Neurosci. 7, 1271–1278.

Wager, T.D., Phan, K.L., Liberzon, I., Taylor, S.F., 2003. Valence, gender, and lateralization of functional brain anatomy in emotion: a meta-analysis of findings from neuroimaging. Neuroimage 19, 513–531.

Weyers, P., Muhlberger, A., Hefele, C., Pauli, P., 2006. Electromyographic responses to static and dynamic avatar emotional facial expressions. Psychophysiology 43, 450–453.

Wicker, B., Keysers, C., Plailly, J., Royet, J.P., Gallese, V., Rizzolatti, G., 2003. Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. Neuron 40, 655–664.

Williams, L.M., Das, P., Liddell, B., Olivieri, G., Peduto, A., Brammer, M.J., Gordon, E., 2005. BOLD, sweat and fears: fMRI and skin conductance distinguish facial fear signals. Neuroreport 16, 49–52.

Yang, T.T., Menon, V., Eliez, S., Blasey, C., White, C.D., Reid, A.J., Gotlib, I.H., Reiss, A.L., 2002. Amygdalar activation associated with positive and negative facial expressions. Neuroreport 13, 1737–1741.