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Research Report

Interference control during recognition of facial affect enhances the processing of expression specific properties — An event-related fMRI study

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ABSTRACT

Though we can almost pre-attentively categorize the valence of facial expressions, we experience emotional ambiguity when confronted with facial expressions in a context with incongruent emotional information. We simultaneously presented interfering background colors during forced-choice categorizations of negative (fear), neutral and positive (happy) expressions. Conflicting information induced strong and differential interference effects on a behavioral level which was mirrored in comparable activations on a neuronal level. Besides a common fronto-parietal attention network which was activated during interference resolution, we found differential interference effects for facial expressions. Incongruent trials with neutral expressions induced a distinct activation pattern in ventral visual regions particularly involved in deeper analysis for both the task-relevant facial expressions (fusiform (FFA) and occipital face area (OFA)) and the task-irrelevant color (V4). Compared to neutral expressions, incongruent trials including either negative or positive expressions elicited attenuated interference effects. Unlike incongruent trials with positive facial expressions which showed only sparse activation in frontal cortex, interference resolution during processing of negative facial expressions resulted in specific activations in regions (V3a, MT$^+$, STS) which might be involved in processing of implicit dynamics of negative expressions. Thus, functional activations in visual processing regions might specifically be related to processing demands of different expressions.

1. Introduction

From an ecological perspective, facial expressions always appear in a broader temporal and spatial context. Contextual features are often relevant for a unique interpretation of facial expressions, but emotional incongruent contextual features might also introduce ambiguity during recognition of facial expressions.

Several studies by de Gelder and her colleagues (Meeren et al., 2005; Righart and de Gelder, 2006) demonstrated that different components of event-related potentials during emotional face processing are modulated by contextual stimulus features. These authors, for instance, demonstrated a modulation of the visual P1 component by emotional incongruent compounds of facial expressions and emotional body postures (Meeren et al., 2005). Additionally, a modulation of the face-

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specific N170 component depending on the emotional congruence of facial expression and the content of a background scene has been reported (Righart and de Gelder, 2006). Based on the assumption that the visual P1 component putatively originates in extrastriate cortex (Di Russo et al., 2005) and the visual N170 component in temporo-occipital regions (Pizzagalli et al., 2002; Itier and Taylor, 2004), these data point to a modulation of early visual processing by emotionally conflicting material. Furthermore, examining a patient with a right-sided hemianopsia, de Gelder et al. (2005) observed an effect of congruence for fearful facial expressions presented both in the blind and the intact hemifield with a signal increase in the amygdala and fusiform gyrus. These data support the view of a distinctive role of both the amygdala and the fusiform gyrus in face related emotional interference processing.

The studies from de Gelder and colleagues (Meeren et al., 2005; Righart and de Gelder, 2006) suggest a modulatory effect of congruent and incongruent contextual information during categorizing facial expressions which already appears during early processing in extrastriate visual regions. However, modulatory effects of contextual emotional information are not restricted to extrastriate visual processing regions but also seem to include more dorsal brain regions involved in executive control during contextual interference. For example, by introducing task-irrelevant emotional information while maintaining the focus of attention on the non-emotional color of a word (the so-called «emotional Stroop task»), Compton et al. (2003) reported a widely distributed almost left lateralized activation pattern in medial and lateral frontal, inferior parietal, superior and inferior temporal regions as well as in right fusiform gyrus. Furthermore, in a face-word Stroop-like task with conflicting emotional information in both stimulus dimensions, Etkin et al. (2006) separated regions responsible for emotional conflict detection (medial and lateral frontal lobe, amygdala) from the rostral anterior cingulate cortex (rACC). The latter is supposed to resolve emotional conflicts by means of inhibiting amygdala activation. Unfortunately, the functional analysis of this study was restricted to these brain regions allowing no inferences to attentional control mechanisms in posterior brain regions. Egner et al. (2008) confirmed this inhibitory effect of the rACC on the amygdala during emotional conflict resolution.

Therefore, contextual interference during recognition of facial affect seems to involve activations in extrastriate visual, frontal as well as limbic brain regions. More specifically, there seems to be a dynamic interplay between frontal areas in relation to both limbic (Etkin et al., 2006; Egner et al., 2008) and visual brain areas (Compton et al., 2003). Especially the latter coupling seems important since it suggests different levels of conflict control. Whereas fronto-parietal regions may provide more general conflict control, modulatory effects in visual regions might reflect regional competition between the processing of different stimulus features (Desimone and Duncan, 1995) and the promotion of task-relevant stimulus features (Egner and Hirsch, 2005). Explanatory analyses in the study by Egner et al. (2008) revealed activations in posterior occipital, temporal and parietal brain regions, but these activations were rather unspecifically associated with emotional conflict detection and conflict resolution during emotional face processing. Interestingly, non-emotional conflict resolution during face perception resulted in a functional connectivity between the left prefrontal cortex and the fusiform face area (FFA; see Kanwisher et al., 1997) suggesting an enhanced processing of facial stimuli in sensory cortex during task induced interference (see Egner and Hirsch, 2005). This was apparently not the case during emotional conflict resolution. The above mentioned studies by de Gelder and co-workers, however, suggest specific modulatory effects of emotional incongruent contextual features on categorizing emotional expression in extrastriate visual cortex. More specifically, valence judgments of facial expression during contextual interference should involve activations in specific visual regions which promote the processing of specific emotional expressions. In this case, functional activations in extrastriate visual regions responsible for processing featural and configural aspects of specific emotional expressions might be specifically rather than unspecifically necessary for a proper judgment of these expressions.

To examine whole brain physiological aspects of processing emotional interferences we developed an experimental task design which should allow to separate contextual interference processing from emotional face processing. More specifically, we were interested in brain regions which are involved in both general interference resolution and specifically in the processing of the task-relevant facial

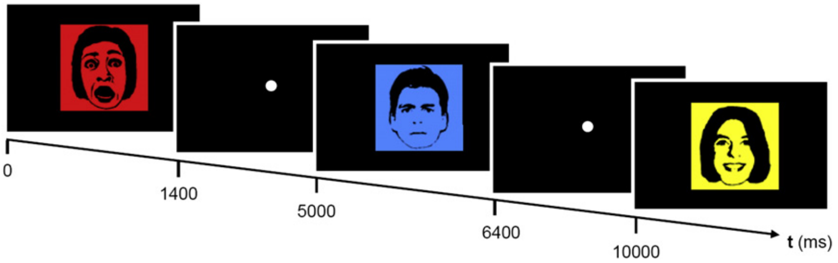

Fig. 1 – Temporal cycle of the trial sequence in the second experimental run: each picture was presented for 1400 ms with an ISI of 3600 ms (jitter ± 200 ms). Subjects were asked for a fast and accurate classification of the emotional valence of negative, neutral, and positive expressions in a three-alternative forced-choice categorization. In a preceding run, subjects had to rate the valence and arousal of facial expressions where negative expressions were systematically combined with a red, neutral expression with a blue and positive expressions with a yellow background color. In the second run, these face–color-combinations were repeated (congruent trials; examples are shown in the figure) or systematically changed (incongruent trials).

expressions. Therefore, we introduced a second low-level feature emotional stimulus dimension to create a conflict in emotional processing during a categorical judgment of the valence of facial stimuli (see Fig. 1 for stimuli, trial sequence and task instructions). Thus, in the task design of the present study pictures of negative (fear), neutral and positive (happiness) facial expressions were simultaneously presented in combination with specific background colors. These background colors were implicitly associated with specific emotional valences during a first experimental run. Though in everyday social interactions we do not regularly encounter facial expression in a colored context, these social situations often contain stimulus features with specific emotional associations. Advertisement, for example, is full of different facial expressions and simple stimulus features, such as colors. Over the life course, we learn to associate colors with specific emotional meanings (Elliot and Maier, 2007), a fact that is often utilized by product placement strategies.

Therefore, in the present experiment, we assumed that the emotional association as well as low-level processing character of these background colors will induce substantial interference effects which even might bias competition in early visual processing stages. Furthermore, this activation in early visual areas might critically and differentially depend on the valence of facial expressions. We, therefore, included negative, neutral and positive expressions in the present experiment. The categorization of positive expressions, for example, strongly relies on specific facial features (Williams et al., 2001; Green et al., 2003). Attention to these features might be enhanced when emotional expressions have to be categorized during contextual interference. This enhanced processing of facial features is indicated by the above mentioned modulatory influences on early visual ERP components (Meeren et al., 2005; Righart and de Gelder, 2006) but allows only a coarse estimation of the spatial distribution of involved visual areas. Functional imaging studies found only unspecific activations in visual areas (Etkin et al., 2006; Egner et al., 2008), but mainly focused on frontal brain regions associated with interference control mechanisms. However, we assumed that these reported frontal areas act specifically in concert with circumscribed visual processing areas.

According to the hypothesis of a distributed interplay between remote brain areas we tried to examine different hypotheses within the present experiment: (1) we considered two systems for regulating attentional control in contextual interference resolution during recognition of facial affect. The first system of attentional control (1a) comprises a fronto-parietal network involved in top-down attentional control by focusing or shifting selective attention to the task-relevant facial expression or inhibiting the processing of the task-irrelevant color information (Banich et al., 2000; Behrmann et al., 2004). More specifically, depending on the processing demands of emotional and neutral facial expressions we expected a differential activation pattern associated with interference resolution during processing of facial expressions (e.g., Williams et al., 2001; Green et al., 2003; Leppänen and Hietanen, 2004). Emotional expressions have been assumed to be processed pre-attentively (Vuilleumier et al., 2001) and efficiently (Green et al., 2003; Leppänen and Hietanen, 2004). This preference in processing of emotional expressions might attenuate the impact of contextual interference when compared to neutral expressions and, consequently, less interference control has to be exerted by fronto-parietal brain regions. The second system of attentional control (1b) covers ventral brain regions, such as the amygdala or the ventromedial prefrontal cortex (VMPFC), which is supposed to detect salient events which could be of task-related importance (e.g., Vuilleumier et al., 2004; Carretié et al., 2005). In particular, the task-irrelevant but emotionally associated background color should convey important emotional information which might attract attention. In case of emotional incongruent information, the amygdala might be sensitive to emotional inconsistencies (see Whalen, 1999), but also to contextual information when facial expressions signal less clear emotional information (Kim et al., 2004). Furthermore, a bottom-up network comprising the temporo-parietal and inferior frontal cortex has been proposed to detect salient events, and which is assumed to be a circuit breaker of top-down attentional control (Corbetta and Shulman, 2002).

(2) The second hypothesis, referred to as «local» control hypothesis, is based on electrophysiological studies showing contextual modulation on emotional face processing in extrastriate regions (Meeren et al., 2005; Righart and de Gelder, 2006). Electrophysiological studies, however, provide only poor spatial resolution to locate early effects in visual brain regions. We, therefore, used functional magnetic resonance imaging (fMRI) to investigate specific extrastriate brain regions involved in attentional control for contextual influences during face processing. There is evidence for selective attentional processes which already affect extrastriate visual

Table 1 – Behavioral data.

		Facial expressions		
		Negative	Neutral	Positive
Reaction time (ms)	Congruent	841 (110)	860 (125)	819 (66)
	Incongruent	936 (92)	990 (143)	904 (56)
Error (%)	Congruent	11.00 (8.91)	10.16 (13.29)	5.61 (4.40)
	Incongruent	20.83 (11.98)	26.66 (12.18)	10.83 (10.58)
Type-of-error (%)	Specific	14.00 (1.26)	20.33 (2.31)	7.83 (1.21)
	Unspecific	6.83 (6.79)	6.33 (.66)	3.00 (1.23)

Mean reaction times and percent error rates for incongruent and congruent trials, and percentage of specific (primed by the background color) and unspecific errors (unrelated to the background color) for incongruent trials. Standard error of the mean (SEM) in brackets.

Table 2 – Regions of significant activation for the [incongruent>congruent] contrast of each emotional category exclusively masked by the respective color contrast at the same statistical threshold.

Brain region	Right/left	BA	Cluster size	T	x	y	z
Negative expressions							
Frontal lobe							
Middle frontal gyrus	L	6	43	3.89	−36	1	61
	L	10	23	3.73	−46	49	9
	L	11	233	5.04	−44	50	−13
	L	47		3.91	−50	46	−6
Inferior frontal gyrus	L	9	414	4.25	−53	17	32
	L	9		4.03	−46	11	27
	L	47		3.62	−42	40	−19
	R	9	222	4.18	48	13	23
Parietal lobe							
Superior parietal lobule	L	7		5.11	−26	−63	51
	L	7	5069	5.45	−28	−64	40
Precuneus	L	7		4.86	−12	−69	53
Temporal lobe							
Inferior temporal gyrus	L	37		3.29	−55	−55	−2
	L	37	524	5.03	−44	−58	−4
	R	20	1516	4.64	57	−41	−10
Fusiform gyrus	L	37		4.24	−48	−51	−13
	R	37		4.55	42	−42	−18
	R	37		4.26	50	−63	−14
Occipital lobe							
Middle occipital gyrus	L	18	36	3.50	−40	−87	1
Lingual gyrus	R	18	237	4.57	14	−85	−23
Subcortical regions							
Thalamus	L		19	3.60	−10	−15	6
Cerebellum							
Pyramis	L		44	3.76	−10	−83	−28
	L			3.38	−24	−60	−27
Uvula	L		54	3.42	−32	−69	−25
Neutral expressions							
Frontal lobe							
Medial frontal gyrus	R	8	161	4.15	2	24	45
Superior frontal gyrus	L	11	10	4.32	−24	40	−19
Middle frontal gyrus	L	9	696	6.59	−55	21	30
	L	11	391	5.40	−42	50	−14
	R	6	51	4.18	44	8	53
	R	10	197	5.28	44	56	−4
	R	11		3.78	42	56	−13
	R	11	15	3.85	38	40	−20
	R	46	638	5.12	59	28	23
Inferior frontal gyrus	L	44		3.39	−46	9	18
	L	46		3.68	−51	39	9
	L	47	30	3.46	−28	23	−8
	R	9		4.49	42	9	25
	R	45		3.56	48	14	14
	R	47		3.85	51	42	−14
	R	47	145	3.73	32	23	−6
	R	47		3.54	50	23	−15
	R	47		3.49	42	24	−20
Parietal lobe							
Superior parietal lobule	L	7	2047	5.18	−26	−60	40
	L	7		4.86	−10	−73	53
	R	7	604	4.31	32	−60	44
	R	7		4.16	30	−69	55
	R	7	73	4.00	14	−71	55
Intraparietal sulcus	R	7		3.97	32	−52	47
Inferior parietal lobule	L	40		4.87	−48	−37	42
Temporal lobe							
Fusiform gyrus	L		22	3.69	−48	−50	−23
	L		13	3.38	−38	−58	−20
Occipital lobe							
Lingual gyrus	L	17		5.52	−18	−84	−1

Table 2 *(continued)*

Brain region	Right/left	BA	Cluster size	T	x	y	z
	L	18	6324	6.34	0	−83	1
	R	18		5.77	10	−82	−4
Cerebellum							
Pyramis	L		56	4.55	−38	−66	−34
	R		69	3.63	12	−79	−25
	R		10	3.40	34	−70	−34
Positive expressions							
Frontal lobe							
Superior frontal gyrus	L	6	18	3.62	−22	−5	65
Middle frontal gyrus	L	6	22	3.50	−30	−1	55

All reported regions are significant at $p<.001$ (uncorrected) with a spatial extent threshold of $k=10$. Abbreviations: BA = Brodmann area; x, y, z = coordinates of peak activations in Talairach coordinates.

processing stages by promoting task-relevant in spite of task-irrelevant stimulus features (Desimone and Duncan, 1995). Thus, distraction from emotional face processing should be associated with activations in extrastriate regions which indicate the processing of specific stimulus features depending on the processing of specific emotional expressions. Under task conditions of contextual interference, those stimulus features should be biased which allow for a proper valence judgment of facial expressions.

2. Results

2.1. *Behavioral data*

We compared incongruent and congruent trials (congruence) in each of the three valence categories of facial expressions (emotion: negative, neutral, positive). For each subject we computed mean reaction times (RTs) including only trials with correct responses within a time window of 150–2000 ms (see Table 1). Kolmogorov–Smirnov tests on RTs and error data did not reach significance (all $p>.134$) thus indicating no violation of the assumption of a normal distribution of the behavioral data.

A 3 (emotion) × 2 (congruence) repeated measure ANOVA for RTs revealed main effects for both the factor emotion ($F_{2,38}=3.77$, $p=.032$) and the factor congruence ($F_{1,19}=68.91$, $p<.001$). Post-hoc Bonferroni adjusted comparison showed that RTs for incongruent trials (944 ms, SEM = 18) were significantly increased compared to congruent trials (840 ms, SEM = 19; $p<.001$). There was also a significant emotion × congruence interaction ($F_{1.5,28.6}=4.46$, $p=.018$, Greenhouse–Geisser (GG) corrected) elicited by a stronger increase in RTs for incongruent trials with neutral expressions. Paired *t*-tests comparing RT differences between the congruent and incongruent condition in each emotional category confirmed a strong interference effect for each contrast (negative $t_{19}=6.77$, $p<.001$; neutral $t_{19}=6.70$, $p<.001$; positive $t_{19}=6.87$, $p<.001$).

An almost identical pattern was obtained for percent error rates for misclassifying facial expressions (see Table 1). A repeated measure ANOVA showed significant main effects for the factors emotion ($F_{2,38}=5.22$, $p=.010$) and congruence ($F_{1,19}=44.38$, $p<.001$), and a significant emotion × congruence interaction ($F_{2,38}=1.54$, $p<.001$) explained by stronger effects of incongruence with neutral expressions. Paired *t*-tests showed interference effects for the negative ($t_{19}=4.51$, $p<.001$), neutral ($t_{19}=7.39$, $p<.001$), and positive emotional category ($t_{19}=2.67$, $p=.015$) by comparing the congruent and incongruent trials in each category.

To specifically address erroneous task performance during contextual interference in incongruent trials we classified errors in these trials as specific or unspecific errors. This approach should demonstrate that the emotional association of the background colors as implicitly induced in the first experimental run is able to induce specific interference effects, thus, resulting in significantly more specific errors compared to unspecific errors. Specific errors during incongruent trials are primed by the emotional association of the background colors whereas unspecific errors were unrelated to this association of the colors. Unspecific errors only indicate a general inattentiveness to the task. In specific errors, however, the background color induced a specific erroneous response due to its emotional association which is incongruent to the valence of the simultaneously presented facial expression. Specific and unspecific errors during incongruent trials were subjected to a 3 (emotion: negative, neutral, positive) × 2 (type-of-error: specific, unspecific) repeated measure ANOVA. There was a significant main effect for emotion ($F_{2,38}=8.30$, $p=.001$) and type-of-error ($F_{1,19}=76.58$, $p<.001$) as well as a significant emotion × type-of-error interaction ($F_{2,38}=5.89$, $p=.006$). Post-hoc Bonferroni adjusted comparison revealed that specific errors (14.06%, SEM = .90) were significantly higher compared to unspecific errors (5.50%, SEM = .62; $p<.001$). In particular, specific compared to unspecific errors during categorizations of neutral expressions were more strongly increased ($t_{19}=7.63$, $p<.001$) compared to negative ($t_{19}=3.56$, $p=.002$) and positive expressions ($t_{19}=2.93$, $p=.009$; see Table 1).

2.2. *Imaging data*

In a first approach, we analyzed interference effects in each emotional category and we compared incongruent against congruent trials for each emotional category masked by the respective color contrasts (see Table 2 and Fig. 2). Incongruent trials with negative expressions were associated with a significant signal increase in left middle and bilateral inferior

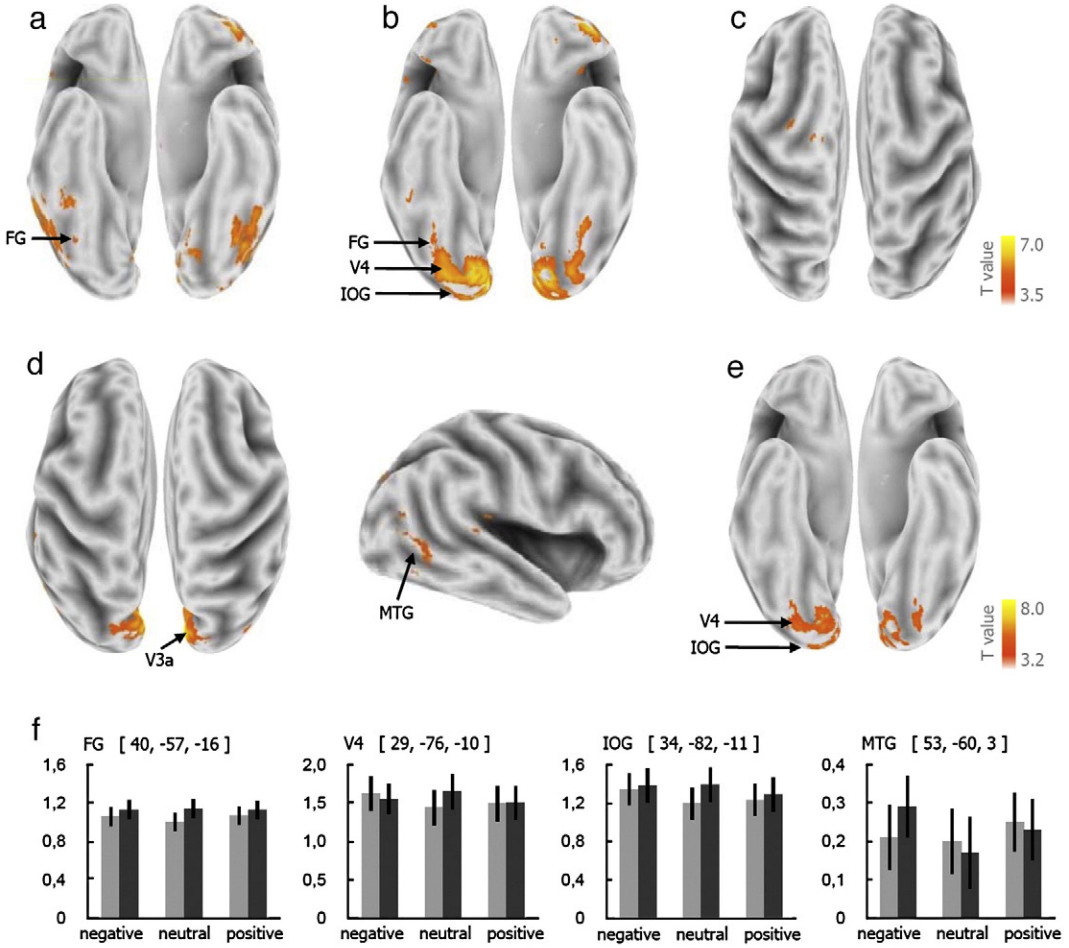

Fig. 2 – Functional activation for the [incongruent>congruent] contrasts for (a) negative, (b) neutral and (c) positive expressions ($p<.001$, uncorrected, $k=10$). Only sparse left frontal activations were found for incongruent trials with positive expressions. Incongruent trials with negative and neutral expressions revealed specific activation patterns in extrastriate visual regions (right FG (~FFA)) for both negative and neutral expressions and in V4 and IOG (~OFA) for neutral expressions. Interaction analyses confirmed these specific activations. Incongruent trials with (d) negative expressions revealed distinct activations in V3a and right hemispheric MOG (~MT^{+}) and MTG (~STS); incongruent trials including (e) neutral expressions showed specific activations in V4 and IOG (~OFA). (f) Percent signal change for right hemispheric ROIs in FG, V4, IOG and MTG (light bars indicate congruent trials, dark bars indicate incongruent trials). Functional contrasts are rendered on the human Colin atlas implemented in the CARET software (Van Essen et al., 2001). Coordinates refer to the Talairach space (Talairach and Tournoux, 1988); error bars indicate the standard error of the mean (SEM). Abbreviations: FFA, fusiform face area; FG, fusiform gyrus; IOG, inferior occipital gyrus; MOG, middle occipital gyrus; MTG, middle temporal gyrus; OFA, occipital face area; STS, superior temporal gyrus.

frontal gyrus. In posterior regions we observed activations in left superior parietal lobule (SPL) extending to intraparietal sulcus (IPS) and inferior parietal lobule (IPL). Furthermore, we obtained peak activations in ventral (fusiform gyrus) and ventro-lateral temporal regions (inferior temporal gyrus and sulcus) as well as in bilateral brain areas in the antero-medial cuneus.

Incongruent compared to congruent trials with neutral expressions resulted in bilateral activations in middle frontal and right inferior frontal gyrus as well as in right medial and left superior frontal gyrus. Parietal activations were located in bilateral SPL and IPS as well as left-sided activations in the IPL. Additionally, we observed activations in lateral occipital regions in left middle and right inferior occipital gyrus as well as bilateral activations in lingual and fusiform gyrus.

Contrasting incongruent with congruent trials including positive expressions resulted in left-sided activation foci in superior and middle frontal gyrus.

A conjunction analysis including all [incongruent>congruent] contrasts (see Table 3 and Fig. 3) revealed peak activations in right medial, bilateral middle and inferior frontal gyrus and sulcus, in IPS, SPL and inferior parietal lobule (IPL), as well as in bilateral fusiform (BA 19/37) and left inferior temporal gyrus.

An interaction analysis revealed specific activations for incongruent trials with negative and neutral expressions only (see Table 4 and Fig. 2). For incongruent trials with negative expressions there was a bilateral occipital activation pattern medially located in cuneus and lingual gyrus and extending

Table 3 – Regions of conjunct activation including all [incongruent>congruent] contrasts.

Brain region	Right/left	BA	Cluster size	T	x	y	z
Frontal lobe							
Medial frontal gyrus	R	8	30	2.39	6	20	47
Middle frontal gyrus	L	9	169	2.83	−53	23	34
	R	9	166	2.89	40	11	27
Inferior frontal sulcus	L	44	11	3.29	−36	7	29
Inferior frontal gyrus	L	9		2.14	−50	13	27
	L	47	36	2.31	−32	21	−6
	R	47	68	2.49	34	23	−6
Parietal lobe							
Superior parietal lobule	L	7		2.63	−26	−63	57
	R	7	399	2.77	36	−64	49
Intraparietal sulcus	L	40		2.73	−44	−38	48
	L	40	1126	2.80	−34	−45	41
	R	7		2.53	34	−64	35
Inferior parietal lobule	R	40		2.74	36	−54	40
Occipital lobe							
Fusiform gyrus	L	19	12	3.37	−44	−68	−8
	R	19	46	2.53	44	−72	−12
Temporal lobe							
Inferior temporal gyrus	L	37	17	3.35	−46	−57	−6
Fusiform gyrus	L	37	57	2.21	−46	−47	−16
Cerebellum							
Pyramis	R		10	3.57	32	−68	−34

Regions of conjunct activation are significant at $p<.001$ (uncorrected; $T>1.89$, intermediate null hypothesis). Spatial extend threshold was $k=10$.

laterally into the right middle occipital gyrus (MOG). This occipital activation extended ventrally to the right parahippocampal gyrus (BA 19, 30) and dorsally to the right posterior cingulate cortex (BA 30). Additionally, there was a right lateral activation cluster comprising areas of middle and superior temporal gyrus. Incongruent trials including neutral expressions also revealed activation clusters in occipital cortex which were located more ventrally comprising early visual brain regions of the lingual gyrus and cuneus extending ventrally into the fusiform gyrus and laterally into the MOG (BA 18) and the inferior occipital gyrus (IOG, BA 18). An additional cluster of activation was located in right middle frontal gyrus.

We computed percent signal change for different regions of interests (ROI) and compared signal intensity of incongruent compared to congruent trials in each emotional category (paired t-tests, $p<.05$). ROIs derived from the conjunction

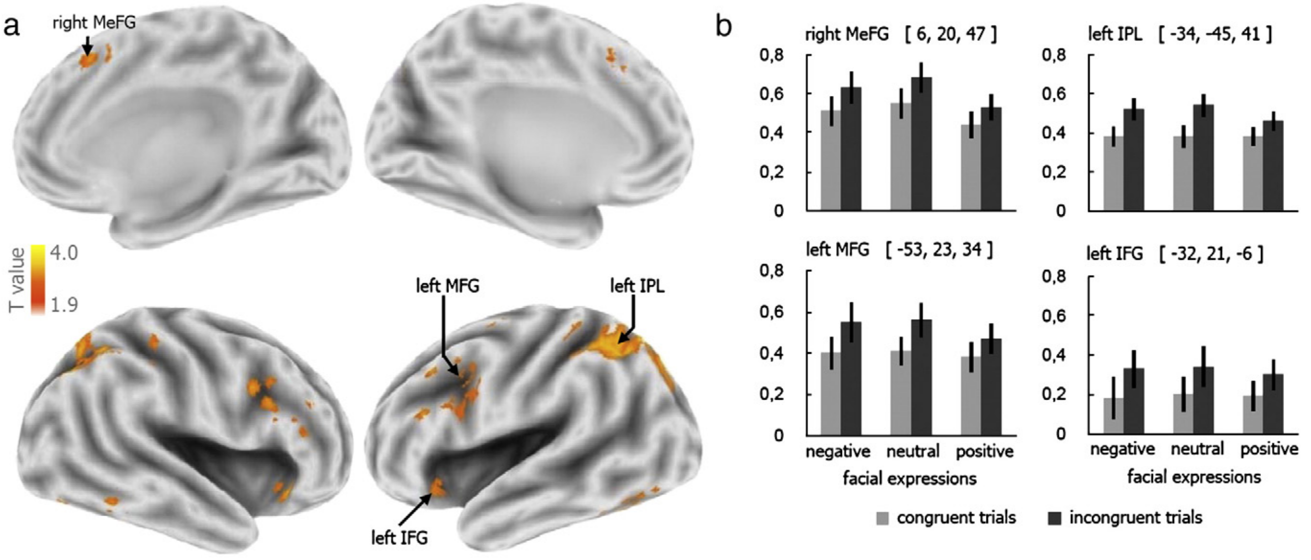

Fig. 3 – Conjunction analysis (intermediate null, $p<.001$, uncorrected, $T>1.89$, $k=10$). (a) Regions of conjunct activations of all incongruent compared to congruent trials. (b) Percent signal change (PSC) in regions of interests (ROIs) determined by the conjunction analysis. The figure shows bar charts for ROIs in right medial frontal gyrus (MeFG), in left inferior parietal lobule (IPL), in middle frontal gyrus (MFG) and in inferior frontal gyrus (IFG). Functional contrasts are rendered on the human Colin atlas implemented in the CARET software (Van Essen et al., 2001). Coordinates refer to the Talairach space (Talairach and Tournoux, 1988); error bars indicate the standard error of the mean (SEM).

Table 4 – Regions of distinct activation as revealed by an interaction analysis for incongruent trials including negative and neutral expressions.

Brain region	Right/left	BA	Cluster size	T	x	y	z
Negative expressions							
Temporal lobe							
Superior temporal gyrus	R	41	34	3.64	40	−30	16
	R	22	10	3.62	67	−34	18
Middle temporal gyrus	R	21	147	3.68	57	−60	1
	R	21		3.42	50	−50	1
Occipital lobe							
Middle occipital gyrus	R	39		3.36	53	−68	9
	R	19	10	3.47	55	−66	−8
Lingual gyrus	L	18		4.27	−10	−75	7
Cuneus	L	18	553	4.43	−2	−86	19
	L	19	33	3.96	−30	−86	37
	R	18		4.33	14	−77	22
Limbic lobe							
Parahippocampal gyrus	R	19	15	3.93	26	−49	−1
	R	30		3.35	20	−46	8
Posterior cingulate cortex	R	30	16	3.75	18	−54	14
	R	30	10	3.53	4	−58	12
Neutral expressions							
Frontal lobe							
Middle frontal gyrus	R	10	14	3.65	44	56	−4
Occipital lobe							
Lingual gyrus	L	17		4.50	−8	−89	6
	R	18		4.58	10	−82	−4
Cuneus	R	17	2203	4.63	16	−91	3

Regions of specific activation are significant at $p < .001$ (uncorrected) with a spatial extent threshold of $k = 10$. Abbreviations: BA = Brodmann area; x, y, z = coordinates of peak activations in Talairach coordinates.
Functional activations were masked by the respective color contrasts at the same statistical threshold.

analysis showed a significant signal increase for all incongruent compared to congruent trials in each emotional face category (see Fig. 3). Neutral incongruent trials led to significantly higher signal increases bilateral in V4, bilateral in the fusiform face area (FFA) and in the right occipital face area (OFA), whereas negative incongruent trials only showed increased signals in bilateral fusiform gyrus and in right middle temporal gyrus (~STS; see Fig. 2). Positive incongruent trials failed to show a significant signal increase in right fusiform gyrus (~FFA, $p = .078$).

3. Discussion

The present study examined neuronal correlates of interfering emotional face processing by background colors which were associated with different emotional valences. Incongruence of emotional valence between facial expressions and background colors induced significant interference effects. Behavioral data indicate that incongruent trials resulted in increased reaction times and decreased response accuracy. The background colors induced specific erroneous responses during incongruent trials due to their emotional association. This was indicated by significantly increased specific compared to unspecific errors. Thus, background colors obviously gained a specific emotional association during the first experimental run and were able to induce specific interference effects during incongruent trials in the second experimental run. Furthermore, in a series of pilot studies (see Section 4.4) iterative valence judgments on the emotional association of these colors additionally indicated that these colors were actually associated with an emotional association as intended by the present experimental procedure. During the course of the experiment colors were increasingly categorized according to the valence association as intended by the experimental procedure.

Differential effects of interference resolution were already apparent on a behavioral level indicated by an enhanced effect of incongruence for incongruent compared to congruent trials with neutral expressions for both RTs and response errors. These differential effects were also reflected in distinct functional correlates of interference resolution during processing of different facial expressions. In accordance with our first hypothesis (1) we found a fronto-parietal network (1a) which was commonly activated by incongruent trials irrespective of the type of facial expression (Section 3.1), but we also revealed differential effects with respect to different facial expression (Section 3.2). The second hypothesis of an attentional system (1b) which acts as a salience detector was not confirmed by our data (Section 3.1). However, we found differential activation patterns in extrastriate visual region depending on the valence of facial expressions (Section 3.3). These extrastriate functional activations most likely indicate the processing of stimulus- and emotion-specific features for a proper valence judgment of facial expressions and correspond to our second hypothesis (2) about local regulatory processes in extrastriate visual brain areas.

3.1. *Common brain regions during interference processing*

Irrespective of the emotional expression, incongruent compared to congruent trials activated regions of a fronto-parietal network which corresponds well to our first hypothesis of top-down attentional control. A conjunction analysis revealed frontal activations in the posterior fronto-median wall (BA 8) which might be associated with performance monitoring (Ullsperger and von Cramon, 2004). While regions in dorsolateral prefrontal cortex (BA 9) have been discussed to be associated with task-related attentional demands (Banich et al., 2000), brain areas in the right ventro-lateral cortex have been shown to support the inhibition of prepotent responses (Aron et al., 2004). Interestingly, incongruent trials did not activate dorsal «cognitive» or rostral «affective» subdivisions of the anterior cingulate cortex (ACC; as proposed by Bush et al., 2000). Recent studies (e.g., Nachev et al., 2005) rather indicate that more superior regions in medial frontal wall are involved in several functions originally assigned to the dorsal ACC (dACC). This evidence is corroborated by Compton et al. (2003) who did not find ACC activation and who argued for practice effects which might diminish conflict-related activations in the ACC. Though Etkin et al. (2006) reported a crucial involvement of the ventral ACC in resolving emotional conflicts, this activation was only present in the case of «high conflict resolution trials» (incongruent trials following incongruent ones). The present data analysis, however, was based on all incongruent trials independent of the nature of the preceding trial. Nevertheless, the present analysis revealed a similar region in medial frontal gyrus (BA 8) to be activated for emotional conflicts as reported by Etkin et al. (2006). Furthermore, Egner et al. (2008) reported an adjacent region in dACC responsible for emotional as well as non-emotional conflict monitoring.

Conjunct activation patterns in posterior parietal cortex represent the posterior part of the fronto-parietal attention network which directly serves the control of selective attention. Egner and Hirsch (2005) assumed that these parietal regions might regulate information flow in extrastriate visual processing streams probably by means of amplifying the processing of the task-relevant stimulus feature (facial expression in the present study). This line of argumentation is supported by the present data indicating a significant activation in bilateral fusiform gyrus particularly in the left hemisphere (BA 37) corresponding to the fusiform face area (FFA). Though the FFA is usually localized in the right hemisphere there are also studies indicating a more bilateral representation in women (e.g., Proverbio et al., 2006).

We expected to find activations in ventral systems especially in regions which signal and promote the processing of specific salient stimuli. Unlike peak activations particularly in right inferior frontal gyrus (BA 47) which might underlie the assessment (Nakamura et al., 1999) or mirroring (Lee et al., 2006) of the emotional quality of the depicted faces, we did not find activations in ventral limbic regions. More specifically, we did not find activations in the amygdala which was shown to promote the processing of task-relevant stimulus properties in a bottom-up manner (Vuilleumier et al., 2004), in particular when facial expressions convey emotional ambiguity (Kim et al., 2003, 2004).The amygdala, however, shows strong signal suppression during consecutive repetition of emotional faces (Ishai et al., 2004) as well as top-down suppression by ventral frontal regions in during enhanced cognitive evaluation of stimuli (Nomura et al., 2004; Etkin et al., 2006; see also Compton et al., 2003). Both of these effects might have contributed to the missing amygdala activation in the present study.

3.2. *Distinct frontal brain areas of interference resolution*

Incongruent trials with positive facial expressions generated only sparse activations in the superior and middle frontal cortex. These regions in the vicinity of the frontal eye field (BA 6) are supposed to maintain and orient the focus of attention (Serences et al., 2005; Thompson et al., 2005). Positive facial expressions have been shown to be categorized fast and accurate (Leppänen and Hietanen, 2004) with less demanding visual scan paths. This visual scanning of positive expressions is focused on distinguishing facial features (Williams et al., 2001), which reduces the processing demands of positive expressions and, therefore, their vulnerability to contextual interference (for the relationship of low working memory demand and decreased distractibility, see Lavie, 2005). Presumably, the lower processing demands of positive faces might shift the locus of interference control to later stages of response selection.

In contrast to incongruent trials with positive expressions, incongruent trials with negative and neutral facial expressions generated enhanced interference effects as indicated by both behavioral data and a frontal and posterior parietal activation pattern. A similar activation cluster for both negative and neutral incongruent trials in the left middle frontal gyrus (BA 9) might result from the task-related adjusting of attentional resources (Banich et al., 2000). Increased activation in this region was related to enhanced (and successful) interference control (see Bunge et al., 2001). Particularly, incongruent trials with neutral expressions might result in an increased demand for interference control and resolution which is also indicated by peak activations in right inferior frontal gyrus. Here, a more caudal activation (BA 47) was associated with the inhibition of prepotent responses due to interfering color information (Aron et al., 2004), and the more rostral part (BA 10, 11) was related to the evaluation of the emotional valence of neutral expressions (Nakamura et al., 1999). The latter argumentation seems plausible since neutral expressions are ambiguous themselves compared to emotional expressions (as also revealed in the pilot studies where neutral stimuli showed a broader distribution of misclassification). This ambiguity might be even enhanced when presented with background colors containing interfering information.

3.3. *Selectively activated visual regions depending on the valence of facial expressions*

In addition to the above described conjunct activation pattern in fronto-parietal regions and in accordance with our «local» hypothesis, interaction analyses revealed regions of distinct activations for both negative and neutral incongruent trials. We found activations in dorsal and ventral visual processing streams and the most prominent activations were found in extrastriate visual areas. Egner et al. (2008) also reported occipital and temporal brain regions to be activated during emotional conflict detection and resolution though these activations seemed to be unspecifically related to both emotional as well as non-emotional conflict detection and resolution. In the present study, however, functional activations in extrastriate visual cortex might reflect specific activations related to the distinct processing properties of neutral as well as of emotional expressions, and this seems to be especially the case for processing emotional expressions during contextual interference.

For incongruent trials with neutral expressions we observed an activation pattern which comprises regions in the lingual gyrus. These regions are supposed to support visual object naming (Kiyosawa et al., 1996) and, more specifically, proper face processing (Tempini et al., 1998). Furthermore, neutral incongruent trials also led to a signal enhancement in regions associated with the processing of stimulus properties of the face–color compounds. We observed a significant signal increase in area V4 probably related to the processing of the task-irrelevant color, but also in the mid-lateral fusiform gyrus (BA 37) and the inferior occipital gyrus (BA 18). These fusiform and occipital activations might result from categorical (FFA) and detailed face processing (OFA) (e.g., Kanwisher et al., 1997; Rossion et al., 2003; Schiltz et al., 2006). Egner and Hirsch (2005) also reported a signal increase in FFA during face perception in trials with contextual conflicting information which according to the authors might reflect a mechanism of selective attentional control.

Beside a feed-forward signal transfer, this activation pattern in ventral visual cortex including activations in V4, OFA and FFA might partly reflect signal re-entry from higher-order visual areas which might serve a more detailed object processing. In addition to a feed-forward signal from OFA to FFA, Schiltz et al. (2006) proposed a reverse signal transfer from FFA (face categorization) to OFA (detailed face processing). Based on the present data for incongruent trials with neutral expressions, we presume a neural scenario with a signal increase in V4 for color processing and FFA for face categorization, but additionally with a biased local top-down suppression from FFA (processing the task-relevant facial expression) to V4 (processing the task-irrelevant background color). Furthermore, we suppose a signal re-entry from FFA to OFA for a proper judgment of emotional face morphology in the case of increased interference. Taken together, since neutral expression signal less expressional distinctiveness both the task-relevant and task-irrelevant stimulus features are processed more deeply to find appropriate information for a valid categorization of facial expressions.

In contrast, incongruent trials with negative expressions activated regions centered in bilateral dorsal cuneus with additional activations in the right middle occipital (BA 39) and middle temporal gyrus (BA 37). Processing negative, high arousing emotional stimuli or novel facial displays is often associated with significant activations in (medial) occipital areas (Lang et al., 1998; Clark et al., 1998). Medial cuneus and precuneus have also been reported to be involved in attention shifting between stimuli features (Le et al., 1998). In addition to these medial occipital activations, we found activations in bilateral dV3/V3a and right V5/MT$^+$ for incongruent trials with negative expressions. These brain areas are assumed to process both real as well as implicit motion induced by static pictures (Vaina et al., 2003; Krekelberg et al., 2005). Some of these brain areas also have been shown to be involved in processing implicit dynamics or changeable stimulus features of facial stimuli (Allison et al., 2000) which might be even extracted during recognition of static emotional expressions as in the present study. According to the «space fragment theory» (Davies and Hoffmann, 2003) even static displays of facial expressions retrieve implicit dynamics of facial morphology which might assist proper face categorization. Furthermore, we found an activation pattern comprising the right middle temporal gyrus and the superior temporal sulcus. The latter area corresponds to the functionally defined region STS (see Allison et al., 2000) comprising the postero-superior and -middle parts of the middle temporal gyrus. The STS region has been discussed to be involved in processing mouth or eye dynamics of emotional expressions (Narumoto et al., 2001). Taken together, processing negative expressions during trials of contextual interference, therefore, seems to activate brain regions which might extract implicit expressional dynamics of negative expressions. Empathic mirroring of these implicit dynamics might help to properly categorize these facial expressions.

3.4. *Conclusions*

Differential behavioral effects of contextual interference during emotional face processing were mirrored on a brain physiological level. A conjunct activation pattern was found in medial and lateral frontal regions and in posterior parietal cortex which is assumed to subserve conflict detection and conflict resolution. Furthermore, we found specific activation patterns depending on the valence of facial expressions. Contextual interference while processing negative and positive facial expressions was markedly reduced when compared to neutral expressions. It was already shown that emotional expressions can strongly capture attention and are partly processed in a pre-attentive manner (e.g., Vuilleumier et al., 2001) and, therefore, might be less prone to contextual distraction. This was clearly indicated by sparse functional interference effects during processing of positive expressions. Compared to neutral expressions, interference during processing of negative expressions also revealed attenuated effects of interference. Still, negative facial expressions may contain some emotional and motivational ambiguity (Whalen, 1999) which probably determines in depth processing of implicit dynamics (V3a, MT$^+$, STS) for a proper valence categorization. Neutral expressions, finally, involve a higher emotional uncertainty making them more vulnerable for interference induced by contextual color information. In order to generate an accurate valence categorization of neutral expressions visual processing requires an enhanced analysis of facial expressions (FFA, OFA) and background color (V4) in more detail. The observed functional activations in extrastriate visual areas for negative and neutral expressions might be specifically related to the essential properties of these expressions.

4. Experimental procedures

4.1. *Participants*

We investigated 23 healthy female students recruited from Bremen University campus. Only females were included in order to prevent confounding effects of gender differences in emotional processing (e.g., Wager et al., 2003). All subjects were right-handed (Oldfield, 1971), had normal or corrected to normal vision and normal color vision (Ishihara color-tables; Ishihara, 1974). No subject presented a neurologic or psychiatric history. Three subjects had to be discarded from further analysis because of technical problems or error rates above chance. The final sample consisted of 20 subjects (mean age 22.7 years, SD=2.25, age range 20–29 years). All subjects gave informed and written consent for their participation in accordance with ethic and data security guidelines of the University of Bremen. The study was approved by the local ethics committee.

4.2. *Stimulus material*

The stimuli were based on photographs of people showing fearful (negative), happy (positive) and neutral facial expressions and which were pictographically reduced to black-and-white colors (see Fig. 1). This pictographically reduction allowed for a better combination of emotional expressions with specific background colors (see below). Though this reduction decreased the ecological validity of these expressions, drawing-like expressions are frequently used in various experiments which deal with facial expression processing. The use of a schematic faces revealed similar results on a behavioral level when compared to natural face images (Leppänen and Hietanen, 2004) and have been shown to elicit similar, though slightly reduced face-specific signals in ventral visual processing regions (Halgren et al., 2000). We only used facial pictures which were correctly classified for at least 50% in a four alternative forced-choice pre-evaluation study including 73 participants (unpublished diploma thesis, Weitzel, 2006, University of Bremen).

We introduced 105 emotional stimuli (53 female, 52 male) for each the negative, neutral and positive emotional face category. Fifteen pictures of each face category were used for the first experimental run and 90 pictures were used in the second experimental run (see below). Faces were combined with a background color for each emotional category (see Fig. 1). Specific colors have been shown to have different emotional associations, but these associations seem to vary between different contexts (Elliot and Maier, 2007). The color «red», for example, seems to signal danger in achievement tasks, but also seems to signal positive social emotions in relational contexts (Elliot and Maier, 2007). Bright colors seem to elicit positive emotions, whereas dark colors elicit negative emotions (Hemphill, 1996) and seem to negatively correlate with arousal intensity (Valdez and Mehrabian, 1994). Whereas the above mentioned studies tried to associate specific colors with specific emotions, Ou et al. (2004) proposed a three-dimensional emotional color space with the dimension color activity, color heat and color weight by using a factor-analytic approach. This approach does not associate specific colors with specific emotions, but rather locates specific colors along this three-dimensional emotional color space. Interestingly, this three-dimensional color space is very similar to a two-dimensional model including pleasantness (valence) and activation (arousal) as proposed by Russell (1979). According to this two-dimensional model, negative and positive stimuli are both classified as highly arousing but differ in their pleasantness.

Based on the data of the aforementioned studies on emotional associations of different colors, we choose background colors which had similar valence and arousal properties compared to the emotional expressions used in the present experiment. Two constraints guided the selection of the colors. First, we tried to find colors with similar brightness but with greatest possible distinctiveness in color hue. In the standard face–color-combinations used in the present study, the red background color (Lab 84, 121, 121; according to the CIELAB color space) simultaneously presented with negative facial expressions (fear) is described as color with high «color activity» and «color heat» (high arousal) as well as high «color weight» (negative valence) (Ou et al., 2004) and is a powerful color to signal danger (Elliot and Maier, 2007). Neutral expressions were combined with a blue (Lab 84, 20, −126) and positive expressions with a yellow background color (Lab 84, 1, 127). Blue colors are described as less arousing (Valdez and Mehrabian, 1994) and with minimal color heat and average color weight and color activity (Ou et al., 2004), and therefore, closely resembles emotional neutrality. The color yellow, especially with strong saturation, is described as positively arousing (Valdez and Mehrabian, 1994) and with average color weight but with high color activity and color heat (Ou et al., 2004). At no time of the experiment participants were told that the background color has any relevance for the experiment.

As a result of a series of pilot studies (see Section 4.4) we decided not to counterbalance the color–emotion-association across subjects. These pilot studies revealed that only the emotion–color-combinations as used in the present experiment induced strong color–emotion-associations and consequently reliable interference effects in the second experimental run. Therefore, interference effects in the present experiment are not simply related to the colors themselves but specifically induced by their emotional association.

The stimuli were projected via a JVC video projector using Presentation®-Software (Neurobehavioral Systems; https://nbs.neuro-bs.com) onto a projection screen positioned at the rear end of the scanner with a viewing distance of about 42 cm. Pictures subtended horizontal and vertically 15° of the visual angle. In the first run pictures were presented slightly above the middle of the screen and the scales for judging the emotional expression were presented beneath the pictures (1.5° distance, font «Arial» on black background, horizontal 19° and vertical 1°). In the second experimental run pictures were presented in the center of the screen.

4.3. Trials and sequence

The aim of the first run was to associate the background colors with the emotional valence of the simultaneously presented facial expression. Colors were chosen which closely resemble the valence and arousal properties of facial expressions to facilitate the process of an emotional association (see Section 4.4). Pictures in the first experimental run were presented in a pseudo-randomized block order with blocks of 7–8 pictures of one specific emotional valence. We used 15 pictures for each of the three emotional categories. Each trial started with a picture displayed for 2000 ms. Subjects had to rate each picture with regard to intensity (arousal) of the depicted emotional expression (a scale with «strong», «middle», «weak» appeared underneath the face with each icon assigned to a response button on a three-button-mouse) and, thereafter, with regard to the emotional valence (scale «negative», «neutral», «positive»). Each scale disappeared after 5000 ms or after button press. Trials were presented with an ISI of 4000 +/− 200 ms and between trials a fixation point (.4 × .4°) was displayed. After 45 pictures we introduced a short 30 s break. Thereafter, all 45 pictures were presented a second time but with a different order of presentation to reinforce the emotional association of the background colors. Subjects were encouraged to perform as quickly and intuitively as possible without too much deliberation.

For the second experimental run we used 90 pictures of each emotional category. In 90 trials – referred to as congruent trials – we used the same emotion–color-combination as in the first experimental run. In 30 trials we changed the background color (15 pictures per each of the two remaining background colors), thus resulting in a different emotion–color-combination (incongruent trials). There were at least 82 trials between the repetition of the same face included in a congruent and incongruent trial, thus preventing from any memory or face identity related effects.

The second run started with nine practice trials to allow accommodation to the new task condition. Participants were asked to make a fast, but still accurate forced-choice categorization for each face with regard to its emotional valence (three-button-mouse: «negative» — index finger, «neutral» — middle finger and «positive» — ring finger). This run consisted of two blocks with 180 trials each resulting in 360 trials in total. Each picture was presented for 1400 ms with an ISI of 3600 +/− 200 ms (see Fig. 1). Pictures were presented in a randomized order with two constraints: (1) each block started with 12 congruent trials without presenting any incongruent trials to further allow the participants to accommodate to the task, and (2), congruent trials following incongruent trials did not present an emotional face with the unattended background color of the preceding incongruent trial in order to avoid confounding effects of negative priming (e.g., Tipper, 1985).

4.4. Pilot studies

We conducted three behavioral pilot studies using similar experimental procedures as described in the former sections. These studies included twenty subjects each and were conducted to find an appropriate experimental design for the present fMRI study. In these pilot studies we first compared interference effects in experimental designs including either unbalanced (25:75) or balanced ratios (50:50) of incongruent compared to congruent trials in the second run. Interference indices were calculated by comparing the reaction time difference between all incongruent and congruent trials divided by the sum of both measures ($INI = [\text{incongruent} - \text{congruent}] / [\text{incongruent} + \text{congruent}]$). Positive values of this interference index indicate increased reaction times for incongruent compared to congruent trials. Interference indices were slightly but not significantly increased in the experiment with an unbalanced ($INI = .036$) compared to a balanced ($INI = .032$) ratio of incongruent trials ($t_{38} < 1$). A one-way ANOVA including interference indices separately calculated for negative, neutral and positive expressions revealed significant differences for the unbalanced ($F_{2,38} = 3.80$, $p = .031$) but not for to the balanced design ($F_{2,38} = 2.32$, $p = .112$). As we were specifically interested in differential effects of contextual modulation we decided to choose the unbalanced design for the present study. This proportion of incongruent trials left was still sufficient for a valid and comparable averaging of hemodynamic responses compared to congruent trials (see Huettel and McCarthy, 2001).

Furthermore, a third pilot study was conducted to test whether background colors will get associated with the emotional valence of the facial expression with which they were combined during the first experimental run. Additionally, we were interested in the specificity of our standard face–color-combinations to induce specific emotional associations of the background colors which we assumed to be facilitated due to the emotional qualities of the colors («color emotion»). Therefore, in a third experiment, we compared the face–color-combinations used in the second pilot study with other face–color-combinations. This experiment included two systematic permutations of the face–color-combinations, with the negative expressions, for example, now combined with the blue or the yellow background color during the first experimental run. We also included iterative valence judgments of the colors before, in-between and after the experiments. Valence ratings of colors were subjected to a 3 (time) × 3 (color) ANOVA. The results showed that only for the standard face–color-combinations used in the present experiment the emotional association of the background colors became significantly stronger during the course of the experiment (factor time: $F_{2,38} = 22.68$, $p < .001$) when compared to the other face–color-combinations (factor time: $F_{2,18} = 2.35$, $p = .125$ and $F_{2,18} = 1.43$, $p = .265$, respectively).

The data of this series of pilot studies showed that only the presently used face–color-combinations induced general and substantial behavioral interference effects in the second run of our experiment. This was indicated by significantly increased interference indices for trials with the standard ($INI = .032$) compared to permutated color trials ($INI = .017$; $t_{38} = 3.75$, $p = .001$). Therefore, we used these standard face–color-combinations instead of counterbalancing face–color-combinations across subjects.

Taken together, the results indicate that only for the standard face–color-combination the colors gained a strong emotional association as intended by the experimental procedure. Thus, it was this emotional association which induced interference effects in the second run. Assuming that the colors alone would have induced interference effects in the second run we most likely would have found comparable interference effects for all face–color-combinations.

4.5. *Image acquisition*

Imaging data were obtained on a 3-T SIEMENS Magnetom Allegra® System (Siemens, Erlangen, Germany) using a T2*-weighted gradient echo-planar imaging (EPI) sequence (44 contiguous axial slices aligned to the AC-PC plane, slice thickness 3 mm, no gap, TR = 2.5 s, TE = 30 ms, FA = 90°, 64 × 64 matrix, FOV 192 × 192 mm, interleaved acquisition), and using a manufacturer supplied circularly polarized head coil to measure changes in blood oxygenation level-dependent (BOLD) signals.

During the second run of the experiment we obtained 804 volumes in total. The first 28 volumes containing task instructions and dummy trials were used to allow the magnetization to reach steady state and were discarded from functional analysis.

4.6. *Image analysis*

We used the statistical parametric mapping software SPM2 (Welcome Department of Cognitive Neurology, London, UK) for preprocessing and statistical analysis of functional images and the MarsBar toolbox (http://marsbar.sourceforge.net) for estimating signal change parameters in regions of interest (ROI) analyses.

Functional images were first corrected for latency differences in slice acquisition to the first slice in each image, and after motion estimation realigned to the tenth image for each data set. Images were then normalized to the Montreal Neurological Institute (MNI) stereotactic EPI template using non-linear basis functions and resampled to 2 mm^3 voxel size. Normalized images were spatially smoothed using an isotropic Gaussian kernel of FWHM 8 mm^3 to decrease differences in individual structural brain anatomy and to increase the signal-to-noise ratio. Each onset of stimulus presentation was modeled by a canonical hemodynamic response function (HRF) and its temporal derivative. Images were high-pass filtered (128 s) to remove low-frequency signal drifts.

Nine experimental conditions (3 emotional expressions × 3 colors) were entered into a GLM as regressors. Only trials with correct responses were included, that means, trials where subjects responded correctly with respect to the emotional valence of the displayed expressions and within a time window of 150–2000 ms.

We furthermore added one regressor including erroneous or missed responses and dummy trials. Additionally, six motion correction parameters (resulting from the realignment procedure) as regressors of no interest were also included in the design matrix to minimize false positive activations due to task correlated motion (see Johnstone et al., 2006).

For the first level fixed effects analysis contrasts were specified to examine effects of incongruence for each emotional category (i.e., [negative incongruent > negative congruent]). Furthermore, from all trials included in the second experimental run we randomly choose trials with identical background color of incongruent trials (i.e., trials with identical background colors of incongruent trials including negative expressions) and additionally compared them to congruent trials in each category (i.e., congruent trials including negative expressions). The latter contrasts were used for masking the second level contrasts to eliminate functional activations which were simply due to different background colors of incongruent compared to congruent trials. Both the contrasts comparing incongruent and congruent trials in each emotional category as well as the color contrasts were entered into a second level analysis of variance (ANOVA). Comparisons of incongruent and congruent trials in each emotional category were exclusively masked by the respective color contrast ($p < .001$, uncorrected, $k = 10$; for both the simple contrasts and the mask). To find regions of distinct activations for each incongruent condition in each emotional category we performed an interaction analysis ($p < .001$, uncorrected, $k = 10$) by a subtraction contrast comparing the simple contrast of incongruence of one emotional category with the simple contrasts of the two remaining emotional categories (i.e., [negative incongruent > negative congruent] − {[neutral incongruent > neutral congruent] + [positive incongruent > positive congruent]}). Functional activations revealed by the interaction analysis were also exclusively masked by the respective color contrast at the same statistical threshold. An additional conjunction analysis (intermediate null hypothesis, $p < .001$, uncorrected, $k = 10$) revealed regions of conjunct activation for the incongruence contrasts across all emotional categories.

We additionally performed regions of interest (ROI) analyses for two purposes. First, regions of significant activation in the conjunction analysis were re-entered on first level as functional ROI clusters to extract percent signal change for each subject. We aimed to confirm significant increase of percent signal change ($p < .05$) in each incongruent condition compared to its respective congruent condition on group level in each functional ROI. Secondly, we were particularly interested in activation profiles in specific regions related to the task-relevant (facial expression) and the task-irrelevant stimulus dimension (color). Thus, we defined ROI spheres (radius 5 mm) around centers of masses. The ROIs resulted from combining ROI boxes corresponding to activation coordinates reported in related studies (see below) and the functional activation clusters of the present study. Hence, we «aligned» coordinates in the literature to our specific activation profile. We built ROIs for right hemispheric regions in occipital area V4 (Talairach coordinates $x = 29$, $y = -76$, $z = -10$) which is supposed to predominantly process color information (Bartels and Zeki, 2000). We additionally defined three regions responsible for processing different aspects of emotional expressions: face-specific regions in right fusiform gyrus («fusiform face area» (FFA); $x = 40$, $y = -57$, $z = -16$) and the right inferior occipital gyrus («occipital face area» (OFA); $x = 34$, $y = -82$, $z = -11$, for both see Kanwisher et al., 1997; Gauthier et al., 2000; Rossion et al., 2003; Grill-Spector et al., 2004; Steeves et al., 2005). Furthermore, we defined a functional region in or around the right superior temporal sulcus (STS; $x = 48$, $y = 56$, $z = 5$) (Puce et al., 1998; Hoffman and Haxby, 2000) which is supposed to process different aspects of emotional face morphology.

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