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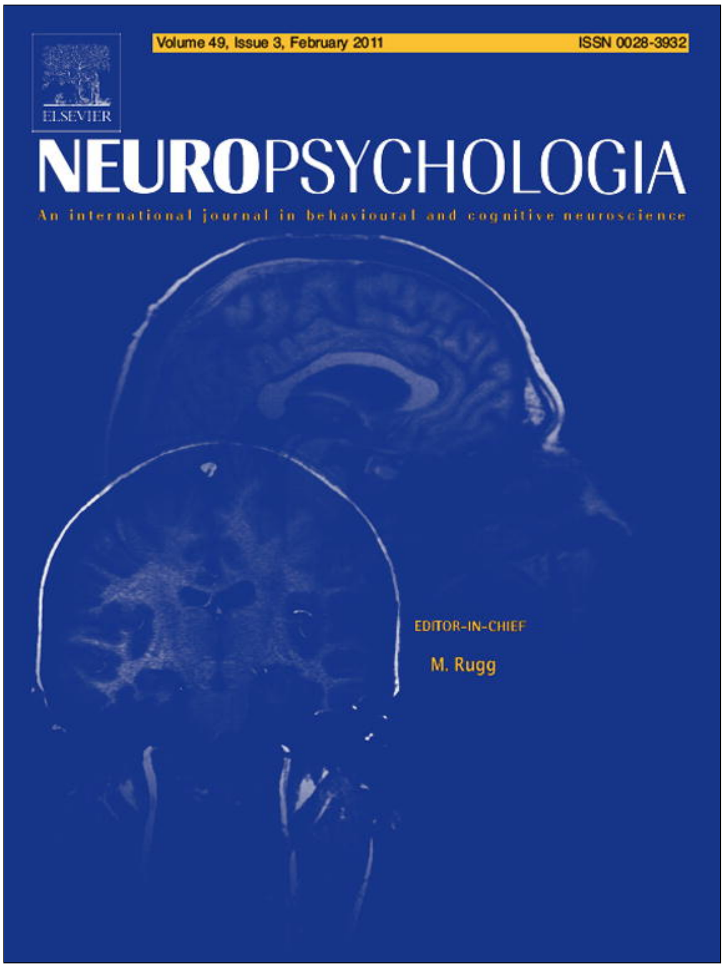

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Neuropsychologia 49 (2011) 416–425

Contents lists available at ScienceDirect

Neuropsychologia

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

Emotional modulation of the attentional blink: The neural structures involved in capturing and holding attention☆

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ARTICLE INFO

Article history:
Received 21 April 2010
Received in revised form
21 December 2010
Accepted 23 December 2010
Available online 30 December 2010

Keywords:
Attention
Attentional blink
Emotion
Amygdala
Orbitofrontal cortex

ABSTRACT

Perceiving a first target stimulus (T1) in a rapid serial visual presentation stream results in a transient impairment in detecting a second target (T2). This "attentional blink" is modulated by the emotional relevance of T1 and T2. The present experiment examined the neural underpinnings of the emotional modulation of the attentional blink. Behaviorally, the attentional blink was reduced for emotional T2 while emotional T1 led to a prolonged attentional blink. Using functional magnetic resonance imaging, we observed amygdala activation associated with the reduced attentional blink for emotional T2 in the face of neutral T1. The prolonged attentional blink following emotional T1 was correlated with enhanced activity in a cortical network including the anterior cingulate cortex, the insula and the orbitofrontal cortex. These results suggest that brain areas previously implicated in rather reflexive emotional reactions are responsible for the reduced attentional blink for emotional T2 whereas neural structures previously related to higher level processing of emotional information mediate the prolonged attentional blink following emotional T1.

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1. Introduction

Our ability to process sequentially presented stimuli is limited. A prominent example is the attentional blink which describes the severe impairment in detecting the second of two targets presented rapidly (i.e., within 500 ms) one after another among a stream of distractor items (Broadbent & Broadbent, 1987; Raymond, Shapiro, & Arnell, 1992). This blink occurs when attentional resources are consumed by the processing of the first target (T1), leaving only few attentional resources available for allocation to the second target (T2; Chun & Potter, 1995; Jolicoeur, 1999; Shapiro, Arnell, & Raymond, 1997). Studies using functional magnetic resonance imaging (fMRI) identified a fronto-parietal network as a locus of the attentional blink in the brain (Hein, Alink, Kleinschmidt, & Müller, 2008; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marcantoni, Lepage, Beaudoin, Bourgouin, & Richer, 2003; Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004; Shapiro, Johnston, Vogels, Zaman, & Roberts, 2007).

There is compelling evidence that emotionally arousing stimuli can overcome, at least partly, the attentional limitations underlying the attentional blink. T2s that are emotionally arousing are significantly better detected than neutral T2s and thus reduce the attentional blink (Anderson, 2005; Anderson & Phelps, 2001; De Martino, Kalisch, Rees, & Dolan, 2009; Keil & Ihssen, 2004; Schwabe & Wolf, 2010). This might reflect faster orienting towards emotional stimuli, prolonged holding of attention for emotional stimuli or both (Vuilleumier, 2005). Bilateral amygdala damage abolishes the enhanced detection of emotionally arousing T2s suggesting that this brain area is critical for the reduced attentional blink for emotionally arousing stimuli (Anderson & Phelps, 2001). To date, there is only one study that examined the neural correlates of the enhanced detection of emotional T2s in healthy humans (De Martino et al., 2009). This fMRI study showed enhanced activity in the rostral part of the anterior cingulate cortex (ACC), an area that shares reciprocal connectivity with the amygdala, that was related to the improved detection of fearful compared to neutral faces.

Recent evidence demonstrates that emotionally arousing stimuli do not always reduce the attentional blink but may also lead to a prolonged attentional blink. In particular, emotionally arousing T1s or emotionally arousing to-be-ignored distractor items decrease the report accuracy for subsequently presented neutral T2s (Arnell, Killman, & Fijavz, 2007; Mathewson, Arnell, & Mansfield, 2008; Most, Chun, Widders, & Zald, 2005; Stein, Zwickel, Ritter, Kitzmantel, & Schneider, 2009). Moreover, emotionally arousing T1s reduce the benefit in detection of emotional T2s (Schwabe & Wolf, 2010). Emotional stimuli are preferentially processed and attract substantial attentional resources (Dijksterhuis & Aarts, 2003; Vuilleumier, 2005). The enhanced processing demands

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doi:10.1016/j.neuropsychologia.2010.12.037

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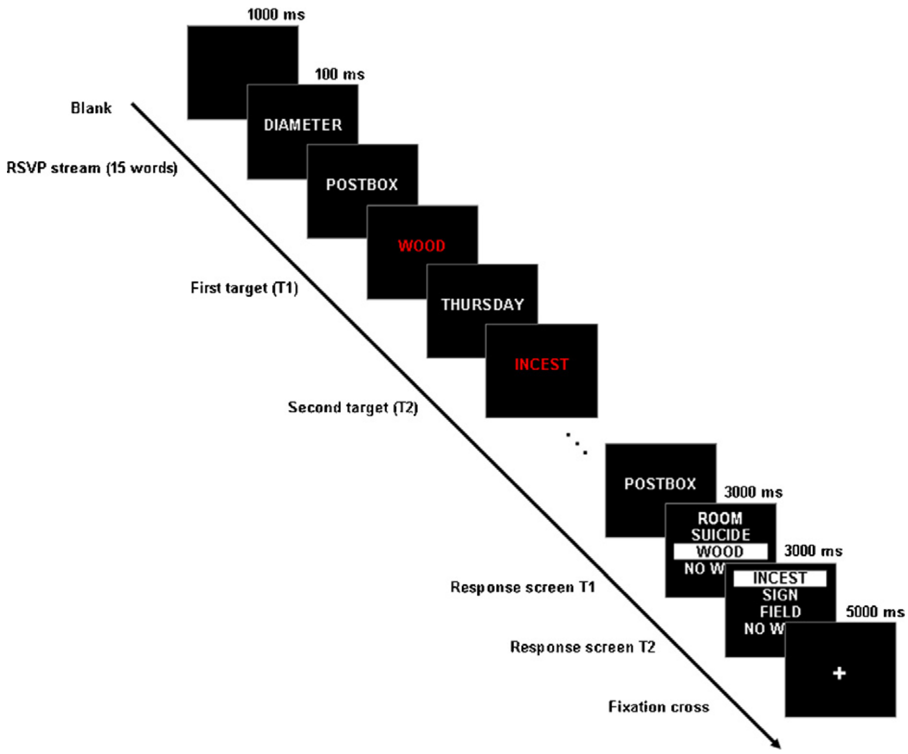

Fig. 1. The rapid serial visual presentation (RSVP) task. Participants searched for target words written in red in a stream of 15 words each presented at fixation for 100 ms with no interstimulus interval. Target words were either neutral or emotional; distractor words were always neutral. There were either one or two target words (T1 and T2, respectively) per trial. If there were two targets, they were either separated by one (early lag, 200 ms; as in the trial shown here) or five (late lag, 600 ms) distractors in the pre-scan session; in the scanning session only the short T1–T2 interval was used. At the end of the RSVP, participants were asked to indicate by key press which of three words was presented as T1 or whether they had no word detected (response screen T1). Thereafter, they were asked to identify the T2 out of three alternatives; if they did not see a second target word they should choose "no word detected" (response screen T2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

associated with emotional T1s leave less attentional capacities for the identification of T2s and thus result in a prolonged attentional blink (Mathewson et al., 2008). The neural circuitry underlying the attentional blink extension by emotionally arousing T1s is still unknown.

In the present experiment, we therefore examined whether the brain structures mediating the prolonged attentional blink following emotional T1s are the same as those involved in the reduced attentional blink for emotional T2s (De Martino et al., 2009). Participants viewed a rapid sequence of 15 words and had to identify two targets (T1 and T2) that were either neutral or emotionally arousing. Based on previous studies (Anderson, 2005; Keil & Ihssen, 2004; Mathewson et al., 2008; Schwabe & Wolf, 2010), we predicted a reduced attentional blink for emotional T2s and a prolonged attentional blink following emotional T1s. At the neural level, we expected that the amygdala would be involved in the enhanced detection of emotional T2s (Anderson & Phelps, 2001). Given that the prolonged attentional blink after emotionally arousing T1s appears to be primarily owing to the extended processing of the emotionally arousing T1s, it is tempting to speculate that prefrontal areas involved in the processing of emotional information (Damasio, 1996; Rolls, Hornak, Wade, & McGrath, 1994) might be associated with the failure to identify the T2 in the presence of emotional T1s.

2. Methods

2.1. Participants

Thirty-eight right-handed, healthy native speakers of German with normal or corrected to normal vision participated in this experiment (19 men, 19 women; mean age: 24.3 years, range: 20–35 years). Participants were prescreened to exclude those with a previous history of psychiatric or neurological illness. All subjects provided written informed consent, and the study was approved by the local ethics committee.

2.2. General procedure

At the beginning of the experiment, participants practiced the rapid serial visual presentation (RSVP) task out of the scanner. This training session, which comprised one trial for each of the 4 T1–T2 combinations at early and late lag and 4 no-T2 trials (see below), served solely to familiarize subjects with the task and was not included in the analyses. Following training, the emotional modulation of the attentional blink was examined in a pre-scan session, in which participants completed 96 trials of the RSVP task. Afterwards, subjects entered the scanner. Here they performed 144 trials of a modified version of the RSVP task that allowed investigating the neural correlates of the emotional modulation of attention during the attentional blink period. All in all the experiment lasted about 90 min.

2.3. Rapid serial visual presentation task

The RSVP task procedure is shown in Fig. 1. Participants searched for two red target words (T1 and T2) that were embedded in a stream of 15 words each presented centrally for 100 ms on a black screen with no interstimulus interval. Distractor words were neutral German nouns written in white. These words were significantly longer than target words (12.0 vs. 5.4 letters) to ensure that the targets were masked by them. T1s and T2s were either neutral (e.g. table, cup, month) or emotionally arousing (e.g. bitch, slave, hate) German nouns that were used in a previous study (Schwabe & Wolf, 2010). In this previous study, we could show that participants experienced the emotional words as significantly more arousing than the neutral words. We used 96 neutral and 96 emotional nouns as T1 and T2, respectively, with the constraint that each word could be used only twice as T1 and T2. Neutral distractor words were randomly selected from a pool of 300 neutral nouns. The words used as alternatives in the test were randomly selected from a pool of 36 neutral and 36 emotional nouns that were never presented as T1 or T2. All words that were used in the present study are shown in Appendix A.

Four T1–T2 combinations were presented: (i) both targets neutral, (ii) T1 neutral and T2 emotional, (iii) T1 emotional and T2 neutral, and (iv) both targets emotional. The position of the T1 varied randomly between the third and seventh position of the stream and there were either 1 or 5 distractors between T1 and T2 corresponding to early (inside the attentional blink period) and late (outside the attentional blink

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period) temporal lags of 200 ms and 600 ms, respectively. Eight trials were presented for each of the 8 T1–T2 condition × lag factor combinations. In addition, there were 32 trials in which no T2 was presented (half of them with a neutral T1 and the other half with an emotional T1), resulting in 96 trials that were presented in random order.

A trial began when the fixation cross disappeared that was presented for a variable time (5000–7400 ms) between trials (Fig. 1). The screen remained blank for 1000 ms before the onset of the RSVP stream which consisted of 15 words (1 or 2 red targets and 14 or 13 white distractors) displayed each for 100 ms. At the end of the RSVP stream, participants were presented two separate response screens for T1 and T2 (Fig. 1). First, they were asked to indicate via a key press on a button response box which of three word alternatives was presented as T1. They could also indicate that they did not see the T1 by choosing the option "no word detected". Earlier studies that examined the neural correlates of the attentional blink used mainly 2 or 3 alternative response formats (e.g. De Martino et al., 2009; Kranczioch et al., 2005; Marois et al., 2004; Shapiro et al., 2007). We have decided here for a 4 alternative response format to reduce the likelihood of guessing and choosing the presented T1 or T2 by chance. The response screen was shown for 3000 ms and the selected option was highlighted. Thereafter, subjects were asked to report which of three given alternatives was shown as T2 or to select "no word detected" if they did not see a T2. The distractor items presented on the response screens were never presented as targets. The emotionality of these distractor items varied randomly and their length was comparable to the length of the targets (5.9 vs. 5.4 letters).

The RSVP task used in the scanner was exactly the same as the RSVP task used in the pre-scan session, with one important exception. In the scanning session, there was no late lag condition but always an early T1–T2 lag because we were primarily interested in the neural mechanisms underlying the enhanced detection of emotional T2s and the reduced T2s detection after emotional T1s in the attentional blink period. Participants completed 24 trials for each of the 4 T1–T2 combinations and 48 no-T2 trials (24 with a neutral T1, 24 with an emotional T1), i.e., 144 trials in total, in the scanner.

2.4. Behavioral analyses

Following the standard procedure in the analysis of RSVP data, trials in which the T1 was not correctly detected were excluded from further analyses (Anderson & Phelps, 2001; De Martino et al., 2009; Keil & Ihssen, 2004). T2 detection accuracy in the pre-scan and scanning sessions was analyzed by separate repeated measures ANOVAs. Performance in the pre-scan session was subjected to a lag (early vs. late) × T1 (neutral vs. emotional) × T2 (neutral vs. emotional) ANOVA. As the T1–T2 interval was held constant at 200 ms in the scanning session the behavioral data from this session were submitted to a T1 × T2 ANOVA.

2.5. Image acquisition

Participants were scanned on a 1.5 T whole-body tomograph (Siemens Symphony [Erlangen, Germany], with a quantum gradient system) with a standard head coil. Structural image acquisition consisted of 160 T1-weighted sagittal images (MPRage, 1 mm slice thickness). For functional imaging, we acquired 866 T2*-weighted images covering the whole brain using an echo-planar imaging (EPI) sequence (25 slices; descending slice procedure; repetition time (TR) = 2.5 s; echo time (TE) = 55 ms; 90° flip angle; matrix: 64 × 64; slice thickness: 5 mm; gap: 1 mm; field of view (FOV): 192 mm × 192 mm). Prior to functional scans, a gradient echo fieldmap sequence was measured for B0-correction with the same image geometry.

2.6. Image analyses

Image preprocessing and analyses were performed using the Functional Magnetic Resonance Imaging of the Brain (FMRIB) Software Library (FSL 4.1.4: www.fmrib.ox.ac.uk/fsl). The first three volumes of each participant's EPI were discarded because of an incomplete steady state of magnetization. Preprocessing included B0 unwarping, motion correction and, slice time correction. Data were spatially smoothed using a 5 mm full-width half-maximum Gaussian kernel.

For each subject a general linear model was estimated. Regressors of interest were constructed by a stick function convolved by a hemodynamic response function (HRF) and the first derivative of the HRF, respectively. The following regressors were included: Hit and Miss for each combination of emotional and neutral T1 and T2; correct rejections, false alarms and not detected T1 for emotional as well as neutral T1; key presses, response screen, blank screen, as well as six regressors counting information about motion correction. The data were filtered in the temporal domain using a nonlinear high-pass filter with a 128 s cut-off. Time-series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). Contrast estimates were calculated for Hit minus Miss (overall and for emotional and neutral T1s as well as emotional and neutral T2s separately), T1emotional minus T1neutral and T2emotional_Hit minus T2neutral_Hit by using the adequate regression estimates. Contrast images were registered to individual anatomical images and further to the standard space of the Montreal Neurological Institute brain (MNI-152) using FLIRT (Jenkinson, Bannister, Brady, & Smith, 2001; Jenkinson & Smith, 2001). Registration from high resolution structural to standard space was refined using FNIRT nonlinear registration (Anderson, Jenkinson, & Smith, 2007a, 2007b).

On the group level statistical analyses of the individual contrasts were done using FLAME (FMRIB's Local Analysis of Mixed Effects) stage 1 (Beckman, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckman, Jenkinson, & Smith, 2004) with a random effects model for one sample T-tests. Z (Gaussianised T) statistic images were thresholded using clusters determined by $Z > 2.3$ and a corrected cluster significance threshold of $\alpha = 0.05$ (Worsley, 2001). Additionally, trends up to a threshold of $p \le .20$ are reported because the statistical power for some of the contrasts was relatively low. We employed explorative whole brain as well as region of interest (ROI) analyses. A priori ROIs were the ACC, the amygdala, the orbitofrontal cortex and the insular cortex which were identified in previous neuroimaging studies on the emotional regulation of attention (Bishop, Duncan, & Lawrence, 2004; Bush, Luu, & Posner, 2000; De Martino et al., 2009; Dolan, 2002; Vuilleumier, 2005). The referring masks were taken from the Harvard–Oxford cortical and subcortical atlases delivered with FSL. Four participants had to be excluded from the fMRI analyses because they did not miss any T2. In addition, two participants had to be excluded because of excessive movement, thus leaving 32 participants (16 men, 16 women) in the fMRI analyses.

3. Results

3.1. Pre-scan session: emotional modulation of the attentional blink

In the pre-scan session, participants showed a robust attentional blink as expressed by a significant increase in T2 detection accuracy from the early to the late lag (58 percent vs. 93 percent, chance: 25 percent; main effect lag: $F_{(1,37)} = 205.3$, $p < .001$; Fig. 2). Emotionally arousing T1s and T2s had opposite effects on the attentional blink. Detection of T2s in the attentional blink period (i.e., at the early

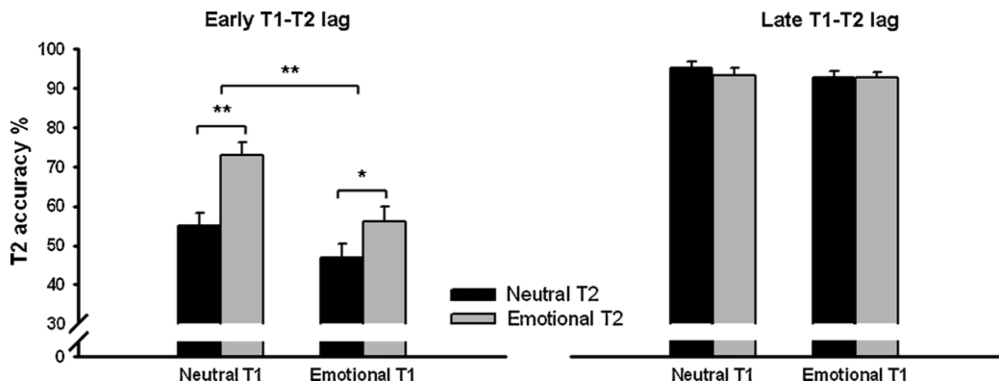

Fig. 2. Detection of the second target in the RSVP stream in the pre-scan session as a function of first and second target (T1 and T2, respectively) emotionality as well as the lag between T1 and T2. T2 detection was significantly impaired at the early (200 ms) compared to the late (600 ms) lag, indicating an attentional blink effect. The attentional blink was prolonged by emotionally arousing T1 and reduced by emotionally arousing T2. Emotionally arousing T1 tended to reduce the effect of the T2 emotionality. Data represent means ± s.e.m.; *$p < .05$; **$p < .001$.

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Table 1
Brain areas more active in response to correctly detected emotional compared to correctly detected neutral T1 and T2, respectively.

Contrast	Brain region	x	y	z	Z-score	Cluster size	p_{corr}
T1emotional – T1neutral	Left orbitofrontal cortex	−44	28	−14	3.66	201	.002
	Left amygdala	−18	−6	−14	2.61	5	.078
T1emotional_noT2 – T1neutral_noT2	Left orbitofrontal cortex	−44	18	−16	4.05	219	.002
	Right orbitofrontal cortex	40	26	−20	2.74	20	.196
	Left amygdala	−18	−10	−12	2.52	7	.066
T2emotional_Hit – T2neutral_Hit	Left orbitofrontal cortex	−44	18	−16	3.48	68	.050
	Left amygdala	−20	−2	−16	2.55	4	.075
T1neutral_T2emotional_Hit – T1neutral_T2neutral_Hit	Left orbitofrontal cortex	−44	28	−14	3.10	104	.022

All p-values are FWE corrected for the respective ROI. Coordinates are given in MNI space.

lag) was impaired by emotionally arousing T1s (T1 × lag interaction effect: $F_{(1,37)} = 11.3$, $p < .005$; T1 effect at early lag: $F_{(1,38)} = 21.6$, $p < .001$) whereas it was enhanced when T2s were emotionally arousing (T2 × lag interaction effect: $F_{(1,37)} = 31.0$, $p < .001$; T2 effect at early lag: $F_{(1,38)} = 34.8$, $p < .001$); the effect of the T1 did not depend on T2 emotionality (T1 × T2 interaction effect: $F_{(1,37)} = 1.5$, $p = .23$) and there was no T1 or T2 effect at late lag (both $p > .30$). As shown in Fig. 2, the facilitating effect of emotionally arousing T2s at early lag was reduced when the T1 was also emotional, yet the referring lag × T1 × T2 interaction effect did not reach statistical significance ($F_{(1,37)} = 2.6$, $p = .11$). In addition, it is noteworthy that the enhanced detection of emotional T2 was a relative enhancement as emotional T2s that were presented in the attentional blink period were significantly less often detected than when they were presented outside of the attentional blink period (65 percent vs. 93 percent; $t_{(37)} = 10.35$, $p < .001$).

The T2 false alarm rate was below 1 percent. For the entire pre-scan session, T1 detection accuracy was 93.8 percent and not influenced by T1 emotionality, T2 emotionality, T1–T2 lag or T2 presence (all $p > .20$).

3.2. Scanning session: neural correlates of the emotional modulation of attention

Behavioral data from the scanning session confirmed the emotional modulation of attention in the attentional blink period (Fig. 3). Emotionally arousing T1s reduced T2 detection (main effect T1: $F_{(1,37)} = 15.3$, $p < .001$). In contrast, a T2 was better detected when it was emotionally arousing compared with when it was neutral (main effect T2: $F_{(1,37)} = 23.0$, $p < .001$). Fig. 3 shows that the impact of the T2 emotionality depended significantly on the emotionality of the T1 (T1 × T2 interaction effect: $F_{(1,37)} = 6.2$, $p < .02$).

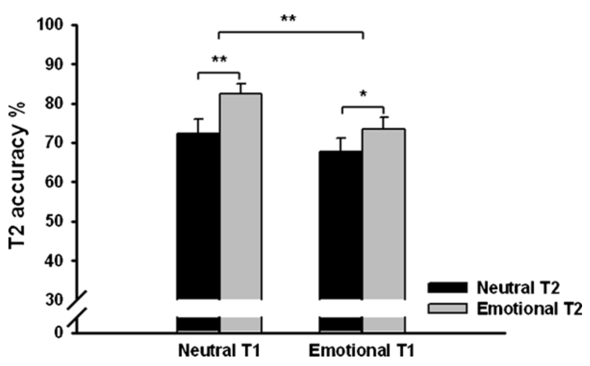

Fig. 3. Detection of the second target in the RSVP stream in the scanning session as a function of first and second target (T1 and T2, respectively) emotionality. Note that the T2 was always presented in the attentional blink period, 200 ms after T1 onset. T2 accuracy was reduced when the T1 was emotionally arousing. Emotionally arousing T2 was better detected than neutral T2. The latter effect was attenuated in the presence of emotionally arousing T1. Data represent means ± s.e.m.; *$p < .05$; **$p < .001$.

The facilitating effect of emotional T2 was reduced when the T1 was also emotional.

Overall, T2 detection accuracy was better in the scanning session than in the pre-scan session (74 percent vs. 58 percent) which may be owing to practice effects or to the lack of a late lag which made the task more predictable and thus easier. Again, the T2 false alarm rate was below 1 percent. In the scanning session, participants were able to detect the T1 in 94.8 percent of the trials. T1 detection was not affected by T1 emotionality, T2 emotionality, T1–T2 lag and T2 presence (all $p > .80$).

3.2.1. Neural structures responding to emotional T1 and T2

Several brain areas showed significantly higher activation in response to emotional compared to neutral T1 and T2. Emotional compared to neutral T1s were associated with greater activity in the left orbitofrontal cortex. Furthermore, there was a trend for increased activation towards emotional compared with neutral T1s in the left amygdala (T1emotional – T1neutral; Table 1). Table 1 shows that the same areas were activated for emotional compared to neutral T1s when we considered only those trials in which no T2 was presented (T1emotional_noT2 – T1neutral_noT2).

The brain areas showing increased activity to correctly reported emotional vs. neutral T2s were very similar. The left orbitofrontal cortex showed greater activation towards correctly detected emotional compared to neutral T2s, a trend was found for the left amygdala (T2emotional_Hit – T2neutral_Hit; Table 1). When we considered only those trials in which the T1 was neutral, significant activation associated with correctly detected emotional vs. neutral T2 was found in the left orbitofrontal cortex (T1neutral_T2emotional_Hit – T1neutral_T2emotional_Hit; Table 1).

There were no significant activations associated with neutral compared to emotional T1s and T2s, respectively (T1neutral – T1emotional, T1neutral_noT2 – T1emotional_noT2, T2neutral_Hit – T2emotional_Hit, and T1neutral_T2neutral_Hit – T1neutral_T2emotional_Hit).

Thus the brain areas responding to emotional T1 and T2 were more or less the same. Please note, that the contrasts that were reported so far reflected the effect of the stimulus emotionality per se, irrespective of the detection performance.

3.2.2. Neural correlates of correct T2 detection

Overall, enhanced activity in the left amygdala was associated with subjects' detection of the T2. For the right amygdala, there was a trend for a significant increase in activation associated with correct T2 detection (Hit – Miss; Table 2).

Interestingly, a different neural network showed increased activity associated with the failure to detect the T2 compared with correct T2 detection. As shown in Table 2, we found enhanced activity for Miss – Hit in the ACC, the insula and the orbitofrontal cortex.

In addition, the exploratory whole brain analyses revealed greater activation in the paracingulate gyrus in the contrast Miss – Hit ($Z = 3.84$, $p_{corr} < .001$; $x = -6$, $y = 18$, $z = 40$).

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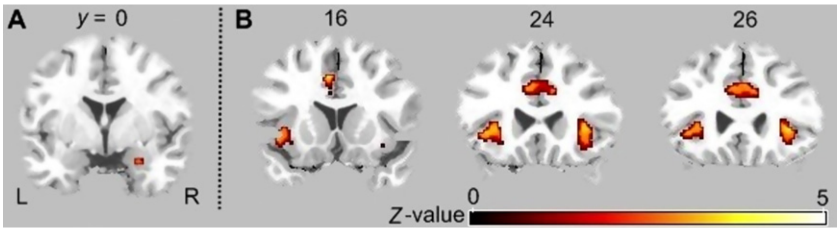

Fig. 4. Brain areas associated with the correct T2 report in the presence of emotionally arousing T1. (A) Enhanced right sided amygdala activity was found for the contrast T1emotional_Hit – T1emotional_Miss. (B) Increased responses in the ACC, bilateral insula and bilateral orbitofrontal cortex in the contrast T1emotional_Miss – T1emotional_Hit.

Table 2
Brain areas associated with successful T2 detection (hit) and the failure to detect the T2 (miss), irrespective of T1 and T2 emotionality.

Contrast	Brain region	*x*	*y*	*z*	*Z*-score	Cluster size	p_{corr}
Hit – Miss	Left amygdala	−26	−6	−22	2.87	27	.027
	Right amygdala	24	−2	−22	2.68	10	.069
Miss – Hit	Anterior cingulate cortex	−4	22	34	3.49	162	.009
	Left insular cortex	−38	24	0	3.82	177	.003
	Right insular cortex	36	22	0	3.94	141	.006
	Left orbitofrontal cortex	−32	26	0	3.50	53	.077
	Right orbitofrontal cortex	34	26	0	3.76	65	.046

All *p*-values are FWE corrected for the respective ROI. Coordinates are given in MNI space.

Table 3
Brain areas associated with successful T2 detection (hit) and the failure to detect the T2 (miss) following neutral and emotional T1.

Contrast	Brain region	*x*	*y*	*z*	*Z*-score	Cluster size	p_{corr}
T1emotional_Hit – T1emotional_Miss	Left amygdala	−26	−6	−22	2.30	1	.109
	Right amygdala	26	0	−24	2.81	15	.056
T1emotional_Miss – T1emotional_Hit	Anterior cingulate cortex	−6	16	38	4.14	333	<.001
	Left insular cortex	−40	16	−2	3.46	157	.004
	Right insular cortex	34	24	2	3.86	101	.015
	Left orbitofrontal cortex	−38	24	−2	3.54	66	.051
	Right orbitofrontal cortex	36	26	0	3.95	96	.019
T1neutral_Hit – T1neutral_Miss	No significant activation						
T1neutral_Miss – T1neutral_Hit	No significant activation						

All *p*-values are FWE corrected for the respective ROI. Coordinates are given in MNI space.

Because the T2 was correctly reported more often when it was emotionally arousing compared to neutral, the detection accuracy (Hit vs. Miss) is confounded with emotionality in the overall activation patterns for Hits vs. Misses. These factors are disentangled in Section 3.2.5.

3.2.3. *Neural correlates of correct T2 detection following neutral and emotional T1*

There was a trend for increased activity of the right amygdala associated with successful T2 detection when the T1 was emotional (T1emotional_Hit – T1emotional_Miss; Fig. 4A and Table 3z). In contrast, the failure to identify the T2 correctly in the presence of an emotional T1 was associated with increased activity in the ACC, the insula and the orbitofrontal cortex (T1emotional_Miss – T1emotional_Hit; Fig. 4B and Table 3). We did not find any significant activation related to the correct T2 report when the T1 was neutral.

3.2.4. *Neural correlates of correct T2 detection for neutral and emotional T2*

The enhanced detection of emotionally arousing T2s was associated with activity in the left amygdala, which showed a stronger activation when emotional T2s were detected than when they were missed (T2emotional_Hit – T2emotional_Miss; Fig. 5A and Table 4). The failure to detect an emotionally arousing T2 was associated with increased activation of the right orbitofrontal cortex, yet this activation did not reach statistical significance after FWE correction (T2emotional_Miss – T2emotional_Hit; Fig. 5B and Table 4).

For neutral T2s, we found a trend for a left sided amygdala activation associated with the correct T2 detection

Table 4
Brain areas associated with successful T2 detection (hit) and the failure to detect the T2 (miss) for neutral and emotional T2.

Contrast	Brain region	*x*	*y*	*z*	*Z*-score	Cluster size	p_{corr}
T2emotional_Hit – T2emotional_Miss	Left amygdala	−28	−10	−16	2.83	15	.046
	Right amygdala	26	−4	−18	2.43	3	.111
T2emotional_Miss – T2emotional_Hit	Right orbitofrontal cortex	34	26	0	3.28	51	.066
T2neutral_Hit – T2neutral_Miss	Left amygdala	−28	−4	−24	2.39	4	.068
T2neutral_Miss – T2neutral_Hit	Anterior cingulate cortex	−6	18	38	3.14	68	.098
	Left insular cortex	−38	16	−2	3.56	180	.005
	Right insular cortex	34	22	0	3.31	56	.061
	Left orbitofrontal cortex	−44	18	−8	3.38	73	.054

All *p*-values are FWE corrected for the respective ROI. Coordinates are given in MNI space.

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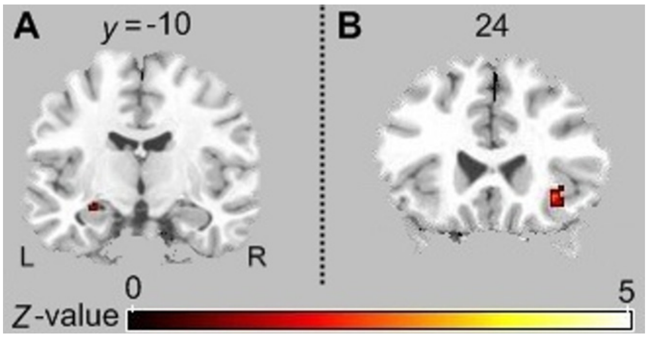

Fig. 5. Brain areas associated with correct report of emotionally arousing T2. (A) Increased activity in the left amygdala was associated with T2emotional_Hit – T2emotional_Miss. (B) Increased activity in the right orbitofrontal cortex was found for T2emotional_Miss – T2emotional_Hit.

(T2neutral_Hit – T2neutral_Miss; Table 4). The failing identification of neutral T2s was again associated with an increased activation of the insula, the left orbitofrontal cortex, and at trend level the ACC (T2neutral_Miss – T2neutral_Hit; Table 4).

No significant activations were found for the interaction contrasts (T1neutral_Hit – T1neutral_Miss) – (T1emotional_Hit – T1emotional_Miss) and (T2neutral_Hit – T2neutral_Miss) – (T2emotional_Hit – T2emotional_Miss) which was most likely due to the high hit rates (and by implication the reduced robustness of the miss trials) in the scanning session.

3.2.5. *Disentangling the effects of target emotionality and detection accuracy*

The behavioral data from both the pre-scanning and the scanning session showed that the emotionality effect of one target stimulus affected the emotionality effect of the other target. Thus, we decided to analyze the activations associated with the T2 detection accuracy in the four T1–T2 combinations separately. The results of these analyses are shown in Table 5. Most importantly, we found a strong trend for a right sided amygdala activation associated with the correct detection of emotional T2s when the T1 was neutral [T1neutral (T2emotional_Hit – T2emotional_Miss)] and a trend for an activation in the ACC, the right orbitofrontal cortex, and the insula associated with the failure to detect emotional T2s that followed emotional T1s [T1emotional (T2emotional_Miss – T2emotional_Hit)]. In addition, there was a trend for increased left sided activation of the insula that was related to the missing of emotional T2s in the face of neutral T1s [T1neutral (T2emotional_Miss – T2emotional_Hit)]. None of the other contrasts approached significance.

4. Discussion

Our behavioral findings replicate previous reports in showing that individuals have considerable difficulties to identify a T2 presented rapidly after a T1 (Broadbent & Broadbent, 1987; Raymond et al., 1992) and that this attentional blink is modulated by the emotionality of T1 and T2 (Anderson, 2005; Anderson & Phelps, 2001; Mathewson et al., 2008; Schwabe & Wolf, 2010). Emotionally arousing T2s reduced the attentional blink whereas emotionally arousing T1s led to a prolonged attentional blink. Furthermore, emotionally arousing T1s reduced the benefit in detection of emotionally arousing T2s suggesting that the processing of emotional T1s leaves fewer attentional resources for allocation to T2s, irrespective of whether the T2 is neutral or emotionally arousing.

Although one previous fMRI study has investigated the neural correlates of the enhanced detection of emotional T2s (De Martino et al., 2009), the present study is the first to examine the neural underpinnings of the opposite effects of emotionally arousing T1s and T2s on the attentional blink. Emotional compared with neutral T1s and T2s (i.e., T1emotional – T1neutral, and T2emotional_Hit – T2neutral_Hit) were associated with increased activity in the amygdala and the orbitofrontal cortex, brain areas that have been related to emotional processing in earlier studies (for reviews see Bechara, Damasio, & Damasio, 2000; Zald, 2002). Interestingly, these structures were differentially involved in the emotional modulation of the attentional blink. Increased activity in the (right) amygdala was associated with the enhanced identification of emotional T2s (i.e., a reduced attentional blink). Activity in the ACC, insula, and orbitofrontal cortex, however, was linked to the failure to detect emotional T2s in the face of emotional T1s (i.e., a prolonged attentional blink).

Two-stage bottleneck models of the attentional blink propose that two discrete stages of processing are required for successful T2 report (Chun & Potter, 1995; Jolicoeur, 1999). In a first, unconscious stage stimuli are rapidly categorized and potentially relevant stimuli are selected. These early representations are not sufficient for subsequent report but may initiate a second, "attentional" stage of processing. In this second stage an early stimulus representation is transferred into a more durable one that allows conscious report. Emotional stimuli are faster detected than neutral stimuli (Öhman, Flykt, & Esteves, 2001; Schupp, Junghöfer, Weike, & Hamm, 2003), i.e., they may be preferentially processed and selected in the first stage. Furthermore, emotional stimuli may be more resistant to masking by surrounding stimuli (Anderson, 2005). In addition to these stage one-processing effects, emotional stimuli are also more thoroughly processed in the second stage (Dijksterhuis & Aarts, 2003; Vuilleumier, 2005) which may be linked to enhanced working memory processes. Therefore, the detection of emotional T2s is enhanced and the attentional blink reduced for emotionally arousing T2s. If however the T1 is emotionally arousing, the enhanced

Table 5
Brain areas associated with successful T2 detection (hit) and the failure to detect the T2 (miss) when the four T1–T2 combinations were separated.

Contrast	Brain region	*x*	*y*	*z*	*Z*-score	Cluster size	p_{corr}
T1neutral (T2emotional_Hit – T2emotional_Miss)	Right amygdala	26	0	–24	2.99	14	.056
T1neutral (T2emotional_Miss – T2emotional_Hit)	Left insula	–30	20	2	2.87	26	.137
T1neutral (T2neutral_Hit – T2neutral_Miss)	No significant activation						
T1neutral (T2neutral_Miss – T2neutral_Hit)	No significant activation						
T1emotional (T2emotional_Hit – T2emotional_Miss)	No significant activation						
T1emotional (T2emotional_Miss – T2emotional_Hit)	Anterior cingulate cortex	–6	16	38	3.12	36	.191
	Left insular cortex	–30	24	0	2.72	19	.182
	Right insular cortex	30	26	4	2.92	22	.162
	Right orbitofrontal cortex	32	20	–14	3.17	42	.084
T1emotional (T2neutral_Hit – T2neutral_Miss)	No significant activation						
T1emotional (T2neutral_Miss – T2neutral_Hit)	No significant activation						

All *p*-values are FWE corrected for the respective ROI. Coordinates are given in MNI space.

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processing of the T1 in the capacity-limited second stage may impede the processing of a subsequent (neutral and emotional) T2 and hence prolong the attentional blink. Our behavioral results are in line with this view. Based on our fMRI data we suggest that different neural structures are associated with the impact of stimulus emotionality on the first and second stage of perceptual analysis and thus that different neural structures are responsible for the attenuation and extension of the attentional blink by emotional stimuli. We suggest that the amygdala mediates the selection of emotional stimuli in the first stage and is therefore responsible for the reduced attentional blink for emotionally arousing T2s while the more thorough analysis of emotional stimuli in the second stage (resulting in a prolonged attentional blink for subsequent stimuli) is mainly dependent on the ACC, the insula, and the orbitofrontal cortex. In other words, we propose that the amygdala is involved in the capture of attention to emotional stimuli whereas the ACC, the insula and the orbitofrontal cortex mediate the holding of attention. Support for this view comes from studies that used binocular rivalry and masking to manipulate awareness and demonstrate that the amygdala is involved in rather reflexive emotional reactions (Dolan & Vuilleumier, 2003; Pasley, Mayes, & Schultz, 2004; Whalen et al., 2004). When stimuli are classified as emotionally relevant, the amygdala recruits a network of connected areas, including the ACC, the insula, and the orbitofrontal cortex (Cavada, Company, Tejedor, Cruz-Rizzolo, & Reinoso-Suarez, 2000; Holland & Gallagher, 1999; LeDoux, 2000), which are then responsible for the further processing of emotional stimuli (Damasio et al., 2000; Dolan, 2002). At this point, it is to be noted that although previous research implicated the amygdala mainly in automatic processing of emotional (especially negative) material, there is some recent evidence suggesting that the amygdala processes emotional stimuli not automatically but flexibly in accordance with the current processing goals (Cunningham, Van Bravel, & Johnsen, 2008; Lien, Ruthruff, & Johnston, 2010).

Our finding that the activity of the amygdala predicted participants' ability to report an emotional T2 (in the face of neutral T1s) correctly is in line with theoretical models that implicate the amygdala in the emotional modulation of the attentional blink (Palermo & Rhodes, 2007; Taylor & Fragopanagos, 2005) and with neuropsychological evidence showing that the benefit in detection of emotional T2 disappears after amygdala damage (Anderson & Phelps, 2001). Previous data indicated that amygdala damage impaired the effects of emotional but not perceptual salience of the AB (Anderson & Phelps, 2001). Thus the role of the amygdala in our study is likely to specifically reflect emotional or motivational salience. Earlier findings showed that the left but not the right amygdala is critical for arousal modulation of the AB for words, which was impaired following left but not right anterior temporal lobectomy (Anderson & Phelps, 2001). At first glance, our results might appear in line with these findings because detection accuracy was in the present study stronger associated with the left amygdala than with the right amygdala. The study by Anderson and Phelps (2001), however, used only neutral T1s and when we considered only the neutral T1 – emotional T2 condition, we found that performance correlated with right but not with left amygdala activity.

Surprisingly, the amygdala was also active in the contrast T2neutral_Hit – T2neutral_Miss which suggests that the amygdala might also support the detection of neutral T2 in the attentional blink period. The reliability of this finding, however, is questioned by the absence of amygdala activation in the T1neutral_Hit – T1neutral_Miss contrast. Moreover, the amygdala activation associated with the detection of neutral T2s disappeared when emotional and neutral T1s were considered separately.

Our results on the role of the ACC in the emotional modulation of the attentional blink might at first glance appear to be contradictory to previous findings. Here, we report that the ACC was associated with the failure to detect emotional T2 while the ACC was previously related to the successful report of emotional T2 (De Martino et al., 2009). In the present study, the amygdala was involved in the enhanced detection of emotional T2 (in the face of neutral T1s). A crucial difference between the present and the previous study (De Martino et al., 2009) is that we presented emotional T1s and T2s whereas there were only emotional T2s in the previous study. As we have argued above, the ACC (together with the insula and the orbitofrontal cortex) may be involved in the enhanced second stage processing of emotional stimuli. This enhanced second stage processing facilitates on the one hand the proposed short-term consolidation of a stimulus (Jolicoeur, 1999) and thus the stimulus detection. On the other hand, however, it increases the threshold for the processing of subsequent stimuli. Thus, the ACC may facilitate the correct report of an emotional T2 when it has not been activated by a previous (emotional) stimulus. If, however, the ACC is already occupied by the processing of an emotional T1, this reduces the likelihood of engaging in the second stage processing of the T2 which in turn reduces the accuracy of T2 report. This idea is supported by our finding that the ACC was associated with the failure to detect emotional T2s if the T1 was also emotional but not if the T1 was neutral.

While we relate the activation of the ACC, the insula and the orbitofrontal cortex to attentional processing, it might also be argued that it reflects participants realizing that they have missed the T2. In particular, the ACC has been associated with performance monitoring by detecting errors (Carter et al., 1998). However, while ACC activations were found in the contrasts T1emotional_Miss – T1emotional_Hit and at trend level in the contrast T2neutral_Miss – T2neutral_Hit, there was no such activation in the contrasts T1neutral_Miss – T1neutral_Hit and T2emotional_Miss – T2emotional_Hit suggesting that the observed ACC activations were at least not solely owing to error detection effects. Moreover, at least for the ACC, activations were much more pronounced in the contrast T1emotional_Miss – T1emotional_Hit, which shows the areas that contribute to the extended attentional blink after emotional T1s, than in the contrast T2neutral_Miss – T2neutral_Hit. In line with this view, the ACC activation in the contrast T2neutral_Miss – T2neutral_Hit disappeared when the T1 neutral and T1 emotional trials were analyzed separately.

Finally, three weaknesses of the present study need to be addressed. First, given the very short T1–T2 interval and the relatively low temporal resolution of fMRI, we can hardly separate the brain activations associated with T1 and T2. Same as other studies investigating the attentional blink and its emotional modulation in the scanner we had to rely on the comparison of trials in which different T1–T2 combinations were realized (De Martino et al., 2009). Second, it is to be noted that the activations we report here are relative activations (in which one T1–T2 combination is compared to another) and no greater than baseline activations. Although previous findings suggest that these relative activations are also associated with greater than baseline activations (De Martino et al., 2009), this conclusion remains relatively speculative based on the present data. Third, we did not include late lag trials and focused solely on the early lag (i.e., the attentional blink period that was most interesting with respect to the purpose of this study) in the scanning session. We decided against a late lag condition in the scanning session because that would have almost doubled the duration of the RSVP task and it appeared questionable if participants could keep their attention for such a long time (about 60 min). The absence of a late lag in the scanning session, however, affects the interpretation of the fMRI findings. For example, it remains unclear whether the observed T2 activation pattern is specific to the attentional blink interval or whether it would also be observed for T2 presented at late lags.

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In summary, the present experiment provides another demonstration of our ability to quickly and efficiently detect emotionally relevant stimuli. Corroborating earlier studies we show that emotional stimuli capture and hold attention which results in a reduced attentional blink for emotionally arousing T2s but a prolonged attentional blink for stimuli presented rapidly after emotionally arousing T1s (Anderson, 2005; Mathewson et al., 2008; Schwabe & Wolf, 2010). Our imaging data indicate that enhanced amygdala activity can account for the enhanced detection of emotional T2s whereas a cortical network (including the ACC, the insula and the orbitofrontal cortex) mediates the impaired detection of T2s following an emotional T1 suggesting that distinct neural structures are involved in capturing and holding attention for emotionally relevant information.

Acknowledgement

This work was supported by a grant of the Rektoratsfonds of the Ruhr-University Bochum.

Appendix A.

Neutral words used as T1 or T2 (translated from German).

Air	Entrance	Plant
Announcement	Episode	Question
Apple	Floor	Rack
Archive	Fork	Role
Article	Frame	Room
Asset	Function	Saloon
Back	Glass	Sand
Bag	Hall	Scantling
Bar	Hand	Script
Basket	House	Sentence
Beaker	Ink	Speech
Bell	Iron	Square
Blackboard	Jar	Stair
Board	Lamp	Stone
Bottom	Leaf	Street
Branch	Leather	Symbol
Can	Line	Table
Cap	Management	Term
Car	Meeting	Text
Card	Meter	Thing
Chalk	Month	Time
Circumference	Motor	Tooth
Coat	Name	Tower
Column	Number	Trousers
Contents	Oven	Umbrella
Contract	Packet	Wall
Country	Page	Water
Cup	Paper	Way
Domain	Pattern	Weather
Door	Pen	Window
Dot	Phase	Wood
Duration	Planet	Word

Emotional words used as T1 or T2 (translated from German).

Abyss	Exitus	Prick
AIDS	Fart	Puke
Alarm	Fat	Purulence
Armor	Fizzling	Quim
Ass	Force	Revenge
Assault	Gaper	Robbery
Bale	Gay	Satan
Balls	Gibbet	Scum
Bane	Gonorrhea	Shit
Bastard	Grub	Slave
Betrayal	Hangman	Slouch
Bitch	Harlot	Sperm
Blain	Hate	Stink
Blemish	Hell	Terror
Bomb	Hitler	Thief
Booger	Hooker	Tick
Bug	Hooligan	Torture
Bunker	Hostage	Tumor
Cadaver	Hunger	Urine
Cheating	Idiot	Vampire
Collapse	Impotence	Victim
Crap	Incest	Violence
Crash	Lie	Virus
Cripple	Loss	Wanker
Cunt	Massacre	War
Death	Mildew	Wart
Devil	Murderer	Weapon
Dildo	Nazi	Whore
Dirt	Panic	Witch
Disgrace	Pest	Wog
Distress	Poison	Wound
Drug	Porno	Zombie

Neutral words used as distractors in the RSVP stream (translated from German).

Absence	Escalator	Population
Acquisition	Event	Positioning
Additive	Extension cable	Predictability
Administration	External communications	Presentation
Advance sale	Fallacy	Presentation
Advertisement	Fence post	Presentation of results
Affability	Fingerpost	Procession
Affirmation	Flagpole	Program
Agreement	Flex	Programming
Airstrip	Floor decking	Publication
Alignment	Flower pot	Question of understanding
Allocation	Foreign word	Questionableness
Announcement	Fork lift	Receptacle
Answering machine	Freezer	Recycle bin
Arbitrary act	Fume hood	Referee
Assembly	Furniture store	Relocation agency
Assignment of dates	Gangway	Remake
Attendance	Garage	Remnants
Auditorium	Garden door	Repetition
Authorization	Gateway	Reservation
Availability	Glove	Restaurant
Backlight	Goalpost	Rinsing agent
Backrest	Group discussion	Roadhouse
Backup	Growing	Roller blind
Balcony furniture	Gym	Roof-deck
Ball pen	Hairpin	Roundtable
Basis for discussion	Hand calculator	Row house
Basis for negotiation	Haystack	Sales booth
Bearing	Headline	Saltcellar
Bookcase	Heating pipe	Scale basis
Book cover	Home	Scale unit
Bootlace	Hosepipe	Schedule
Bottleneck	Imagination	Scratchpad
Box office	Inaugural speech	Screen
Bridge over	In-box	Seconds hand
Briefing	Indication	Service
Brightness	Inducement	Shampoo
Broomstick	Influence	Shipment
Bunch of keys	Ingredient	Shoe sole
Buttonhole	Ink cartridge	Shoulder bag
Caddy	Inventory	Signature
Cake pan	Involvement	Simplification
Calculator	Justification	Slicer
Calendar sheet	Keyhole	Snack-bar
Car tire	Kitchenette	Snow plough
Card game	Ladder spoke	Soft toy
Car-jack	Ladle	Spate stick
Century	Laundry machine	Spinal column
Chair leg	Lens	Stair railing
Chimney	Licensed House	Stamp
Cleaning	Light switch	Station
Clock-face	Line spacing	Stay
Clothesline	Logging	Stirrup holder
Clothespin	Loudspeaker	Store display
Coat hanger	Lounge	Storing position
Coffee cup	Lunch	Straw
Color palette	Mailbox	Summary
Compatibility	Mailing	Sundial
Compendium	Major city	Survey result
Competitive sports	Manifestation	Surveyor's office
Composition	Master	Table of contents

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Compound	Measuring jug	Tape
Connection	Medium wave	Tea bag
Consultation-hour	Membership	Telephone receiver
Contact address	Microgram	Telescope
Contact point	Microphone	Text format
Conveyor	Microwave	Thermometer
Corkscrew	Model car	Thigh
Cost recovery	Morning	Thursday
Countryside	Multi-purpose hall	Time of departure
Crossroads	New release	Topics of conversation
Curtain rod	News	Total number
Cushion	Newsprint	Track
Cutlery	Noise level	Transgression
Data entry	Nomenclature	Transport
Date display	Notepad	Treaty
Dawn	Notification	Tree trunk
Deal	Number pad	Typewriter
Decimal	Nurse	Underlay
Degree of kinship	Object	University calendar
Delay	Observation	Vacuum cleaner
Demonstration	Omission	Vehicle owner
Desk	Opening hours	videotape
Desk top	Out wall	Waiting loop
Destination	Oxygen	Wall paint
Diameter	Page number	Water basin
Diesel engine	Page reference	Water boiler
Difference	Paper-fastener	Water surface
Dinner	Penholder	Water-tap
Disclosure	Peppermint tea	Weather
Distance	Perception	Weather prediction
Distribution	Personnel	Weather report
Drive control	Photo album	Windowsill
Driveshaft	Picture editing	Windshield wiper
Duplication	Picture frame	Winter garden
Employee training	Pin board	Work area
Employer	Pipe tongs	Works meeting
Endurance	Plastic folder	World receiver
Entrance hall	Playback	Wrapping film
Eraser	Playground	Zipper

Neutral words used as foils in the test (translated from German).

Auto	Feather	Pan
Band	Field	Roof
Bottle	Fog	Root
Brace	Format	Shield
Button	Gradient	Sign
Can	Handle	Sole
Cap	Hour	Sound
Chair	Ladder	Space
Circle	Lug	Spoon
Color	Note	Vase
Concrete	Number	Video
Date	Outlook	Wire

Emotional words used as foils in the test (translated from German).

Accident	Fetish	Pussy
Amok	Fool	Racist
Bankruptcy	Fucker	Rejection
Beggar	Hustler	Scab
Burglary	Injection	Suicide
Burning	Lesbian	Slime
Coffin	Louse	Spider
Coma	Nigger	Tits
Corpse	Orgy	Trash
Crisis	Peeper	Vagina
Decay	Piss	Whip
Diarrhea	Plague	Wooer

References

Anderson, A. K. (2005). Affective influences on the attentional dynamics supporting awareness. *Journal of Experimental Psychology: General*, *134*(2), 258–281.

Anderson, J. L. R., Jenkinson, M., & Smith, S. M. (2007). Non-linear optimisation. *FMRIB technical report TR07JA1*.

Anderson, J. L. R., Jenkinson, M., & Smith, S. M. (2007). Non-linear registration, aka spatial normalisation. *FMRIB technical report TR07JA2*.

Anderson, A. K., & Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, *411*(6835), 305–309.

Arnell, K. M., Killman, K. V., & Fijavz, D. (2007). Blinded by emotion: Target misses follow attention capture by arousing distractors in RSVP. *Emotion*, *7*, 465–477.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. *Cerebral Cortex*, *10*(3), 295–307.

Beckman, C., Jenkinson, M., & Smith, S. M. (2003). General multi-level linear modelling for group analysis in fMRI. *NeuroImage*, *20*, 1052–1063.

Bishop, S. J., Duncan, J., & Lawrence, A. D. (2004). State anxiety modulation of the amygdala response to unattended threat-related stimuli. *The Journal of Neuroscience*, *24*(46), 10364–10368.

Broadbent, D. E., & Broadbent, M. H. (1987). From detection to identification: Response to multiple targets in rapid serial visual presentation. *Perception & Psychophysics*, *42*, 105–113.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, *4*(6), 215–222.

Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, *280*(5364), 747–749.

Cavada, C., Company, T., Tejedor, J., Cruz-Rizzolo, R. J., & Reinoso-Suarez, F. (2000). The anatomical connections of the macaque monkey orbitofrontal cortex. A review. *Cerebral Cortex*, *10*(3), 220–242.

Chun, M. M., & Potter, M. C. (1995). A two-stage model for multiple target detection in serial visual presentation. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 109–127.

Cunningham, W. A., Van Bravel, J. J., & Johnsen, I. R. (2008). Affective flexibility: Evaluative processing goals shape amygdala activity. *Psychological Science*, *19*(2), 152–160.

Damasio, A. R. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *351*(1346), 1413–1420.

Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L. B., Parvizi, J., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, *3*(10), 1049–1056.

De Martino, B., Kalisch, R., Rees, G., & Dolan, R. J. (2009). Enhanced processing of threat stimuli under limited attentional resources. *Cerebral Cortex*, *19*, 127–133.

Dijksterhuis, A., & Aarts, H. (2003). On wildebeests and humans: The preferential detection of negative stimuli. *Psychological Science*, *14*, 14–18.

Dolan, R. J. (2002). Emotion, cognition, and behavior. *Science*, *298*, 1191–1194.

Dolan, R. J., & Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. *Annals of the New York Academy of the Sciences*, *1*, 348–355.

Hein, G., Alink, A., Kleinschmidt, A., & Müller, N. G. (2008). The attentional blink modulates activity in the early visual cortex. *Journal of Cognitive Neuroscience*, *21*(1), 197–206.

Holland, P. C., & Gallagher, M. (1999). Amygdala circuitry in attentional and representational processes. *Trends in Cognitive Sciences*, *3*, 65–73.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. M. (2001). Improved optimisation for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, *17*(2), 825–841.

Jenkinson, M., & Smith, S. M. (2001). A global optimisation method for robust affine registration of brain images. *Medical Image Analysis*, *5*(2), 143–156.

Jolicoeur, P. (1999). Dual-task interference and visual encoding. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(3), 596–616.

Keil, A., & Ihssen, N. (2004). Identification facilitation of emotionally arousing verbs during the attentional blink. *Emotion*, *4*(1), 23–35.

Kranczioch, C., Debener, S., Schwarzbach, J., Goebel, R., & Engel, A. K. (2005). Neural correlates of conscious perception in the attentional blink. *NeuroImage*, *24*, 704–714.

LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, *23*, 155–184.

Lien, M. C., Ruthruff, E., & Johnston, J. C. (2010). Attentional capture with rapidly changing attentional controlling sets. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(1), 1–16.

Marcantoni, W. S., Lepage, M., Beaudoin, G., Bourgouin, P., & Richer, F. (2003). Neural correlates of dual task interference in visual streams: An fMRI study. *Brain and Cognition*, *53*, 318–321.

Marois, R., Chun, M. M., & Gore, J. C. (2000). Neural correlates of the attentional blink. *Neuron*, *28*, 299–308.

Marois, R., Yi, D. J., & Chun, M. M. (2004). The neural fate of consciously perceived and missed events in the attentional blink. *Neuron*, *41*, 465–472.

Mathewson, K. J., Arnell, K. M., & Mansfield, C. A. (2008). Capturing and holding attention: The impact of emotional words in rapid serial visual presentation. *Memory & Cognition*, *36*(1), 182–200.

Most, S. B., Chun, M. M., Widders, D. M., & Zald, D. H. (2005). Attentional rubbernecking: Cognitive control and personality in emotion-induced blindness. *Psychonomic Bulletin & Review*, *12*(4), 654–661.

Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General*, *130*(3), 466–478.

Palermo, R., & Rhodes, G. (2007). Are you always on my mind? A review of how face perception and attention interact. *Neuropsychologia*, *45*, 75–92.

Pasley, B. N., Mayes, L. C., & Schultz, R. T. (2004). Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron*, *42*(1), 163–172.

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, *18*(3), 849–860.

Rolls, E. T., Hornak, J., Wade, D., & McGrath, J. (1994). Emotion-related learning in patients with social and emotional changes associated with frontal lobe damage. *Journal of Neurology, Neurosurgery, and Psychiatry*, *57*(12), 1518–1524.

Author's personal copy

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Attention and emotion: An ERP analysis of facilitated emotional stimulus processing. *Neuroreport*, *14*, 1107–1110.

Schwabe, L., & Wolf, O. T. (2010). Emotional modulation of the attentional blink: Is there an effect of stress? *Emotion*, *10*(2), 283–288.

Shapiro, K. L., Arnell, K. M., & Raymond, J. E. (1997). The attentional blink. *Trends in Cognitive Sciences*, *1*(8), 291–296.

Shapiro, K. L., Johnston, S. J., Vogels, W., Zaman, A., & Roberts, N. (2007). Increased functional magnetic resonance imaging activity during nonconscious perception in the attentional blink. *Neuroreport*, *18*, 341–345.

Stein, T., Zwickel, J., Ritter, J., Kitzmantel, M., & Schneider, W. X. (2009). The effect of fearful faces on the attentional blink is task dependent. *Psychonomic Bulletin & Review*, *16*(1), 104–109.

Taylor, J. G., & Fragopanagos, N. F. (2005). The interaction of attention and emotion. *Neural Networks*, *18*(4), 353–369.

Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, *9*(12), 585–594.

Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites. *Science*, *306*(5704), 2061.

Woolrich, M. W., Behrens, T. E. J., Beckman, C., Jenkinson, M., & Smith, S. M. (2004). Multi level linear modelling for fMRI group analysis using Bayesian inference. *NeuroImage*, *21*(4), 1732–1747.

Woolrich, M. W., Ripley, B. D., Brady, J. M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modelling of fMRI data. *NeuroImage*, *14*(6), 1370–1386.

Worsley, K. J. (2001). Statistical analysis of activation images. In P. Jezzard, P. M. Metthews, & S. M. Smith (Eds.), *Functional MRI: An introduction to methods*. Oxford: University Press.

Zald, D. H. (2002). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews*, *41*(1), 88–123.