Rapid visuomotor processing of phobic images in spider- and snake-fearful participants

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Abstract

This study investigates enhanced visuomotor processing of phobic compared to fear-relevant and neutral stimuli. We used a response priming design to measure rapid, automatic motor activation by natural images (spiders, snakes, mushrooms, and flowers) in spider-fearful, snake-fearful, and control participants. We found strong priming effects in all tasks and conditions; however, results showed marked differences between groups. Most importantly, in the group of spider-fearful individuals, spider pictures had a strong and specific influence on even the fastest motor responses: Phobic primes entailed the largest priming effects, and phobic targets accelerated responses, both effects indicating speeded response activation by phobic images. In snake-fearful participants, this processing enhancement for phobic material was less pronounced and extended to both snake and spider images. We conclude that spider phobia leads to enhanced processing capacity for phobic images. We argue that this is enabled by long-term perceptual learning processes.

Keywords: phobia, priming, image processing, amygdala, perceptual learning

Introduction

From an evolutionary point of view, it can be assumed that visual processing and rapid detection of potentially dangerous stimuli in the environment (e.g., perilous animals) is highly adaptive for all humans (cf. Öhman & Mineka, 2001; Öhman, Eriksson, Fredriksson, Hugdahl, & Olofsson, 1974). In addition, that ability should be further enhanced if the given stimulus (e.g., a spider) is interpreted as threatening by one individual (e.g., by a spider phobic) even if the same stimulus is taken as harmless by another non-anxious individual. Empirical evidence indicates that the processing of threatening objects is enhanced in the general population (Fox et al., 2000; Lipp & Waters, 2007; Öhman, Flykt, & Esteves, 2001; Williams, Moss, Bradshaw, & Mattingley, 2005; but see Tipples, Young, Quinlan, Broks, & Ellis, 2002) and for phobic stimuli further pronounced in individuals with specific phobias, (Lipp & Waters, 2007; Öhman et al., 2001; for other anxiety disorders, e.g. social anxiety, see Eastwood et al., 2005; Gilboa-Schechtman, Foa, & Amir, 1999). For instance, in the study by Öhman et al. (2001), non-anxious control participants, spider phobics, and snake phobics had to search for pictures of spiders or snakes in grid-pattern arrays of flower and mushroom pictures, and vice versa. Potentially threatening pictures of spiders and snakes were found more quickly than neutral pictures by all three groups, with even faster performance in the two phobic groups. Furthermore, search times for spider and snake targets but not for neutral targets (flowers and mushrooms) were largely unaffected by the number of distractors (which normally increase response times in serial search tasks), and that effect was further enhanced in phobic participants. These results suggest that detection of phobic pictures might be independent of the number of distractors, indicating an especially high degree of search efficiency (Treisman & Gelade, 1980)[1]. Even though such a “pop out” effect was not consistently found in more recent studies (Yiend, 2010) the evidence points to an information processing advantage for threatening stimuli. This advantage seems to apply not only to the input end, but also to the output end of the processing system: Flykt, Lindeberg, and Derakshan (2012) showed in a similar search task that fear-relevant pictures increased the force with which a response was performed.

But what causes that advantage? Current studies report that the attention of individuals with specific phobias is automatically and involuntarily drawn towards the phobic stimuli. That effect is known as an attentional bias (Mogg & Bradley, 2006; Rinck & Becker, 2006; for reviews see Mathews & MacLeod, 2005; Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van Ijzendoorn, 2007): as a consequence of selective attention, threatening stimuli that are attended are processed faster than unattended ones.[2] Several studies indicate that the attentional bias has a time course where early attentional capture occurs within approximately the first half second of exposure (Asmundson & Stein, 1994; Bradley, Mogg, White, Groom, & de Bono, 1999; Mogg and Bradley, 2006, Rinck & Becker, 2006; but see also Gerdes, Alpers, & Pauli, 2008).

Taken together, there is strong evidence that (1) threatening stimuli are processed faster compared to emotionally neutral stimuli and (2) this accelerated information processing is accompanied by an early attentional bias. But what are the neurophysiological processes underlying accelerated processing? Currently, there are two different accounts which try to explain that phenomenon. First, a widespread assumption is that the human amygdala plays a crucial role in rapid, automatic, and non-conscious processing of threatening stimuli. According to this theory, two cortical pathways are involved when a feared stimulus is recognized: firstly, a slow and elaborate cortical pathway, and

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[1] Note that the efficiency of processing might be further boosted by secondary factors like emotional significance.

[2] Note that the attentional bias may also base on the participants’ expectancy about the appearance of their phobic object/animal (Devue, Belopolsky, & Theeuwes, 2011) or other characteristics of visual perception, for instance, sudden appearance of objects (cf. Cole & Kuhn, 2009, 2010)

secondly, a subcortical route – the so-called ‘low road’ – which projects information directly from the thalamus to the amygdala via the pulvinar. In the latter case, it is assumed that the thalamic input reaches the amygdala more quickly and, therefore, might allow for rapid responses on the basis of limited stimulus information (LeDoux, 1995). This model is supported by recent work from different research teams (e.g., Anderson & Phelps, 2001; Morris, Öhman, & Dolan, 1999), even though some researchers challenge the role of the amygdala in rapid emotional processing (for a review, see Pessoa & Adolphs, 2010). Alternatively to the “low road” hypothesis, the involuntary attentional bias towards fear-relevant stimuli might lead to perceptual learning processes (Kourtzi & DiCarlo, 2006; for a review see Gilbert, Sigman, & Crist, 2001), which in turn might enable faster recognition and encoding of those stimuli (cf. Zeelenberg, Wagenmakers, & Rotteveel, 2006).

As has been repeatedly shown, the classification of natural images by means of speeded motor responses is very rapid (Kirchner & Thorpe, 2006; Thorpe, Fize, & Marlot, 1996). Note that the two accounts described above place different demands on the time-course of the visual processing during this classification. The amygdala account requires the “low road” to (1) classify incoming stimuli according to their emotional relevance, (2) outpace the cortical object recognition route and (3) rapidly modulate that processing route in time for the motor response. In contrast, the perceptual learning account explains enhanced processing of fear-relevant images by long-term changes in the processing hierarchy. Thus, processing enhancement for fear-relevant images could conceivably be hard-wired into those processing structures involved in the first sweep of information processing through that hierarchy (*feedforward sweep*; Lamme & Roelfsema, 2000; VanRullen & Thorpe, 2001). In other words, even if the classification of natural images is already rapid, that of fear-relevant pictures should be further enhanced. A strong prediction of perceptual learning model is that any processing enhancement should be fully present in the earliest signs of visuomotor processing. Therefore, any demonstration of processing enhancements in the earliest motor output would be consistent with a perceptual-learning account and would place strict time constraints on the “low road” account, possibly strict enough to challenge its physiological plausibility.

The goal of the current study was to determine whether accelerated processing of fear-relevant images is detectable at the earliest stages of observable behavior. We used a “response priming” paradigm (Klotz & Neumann, 1999; Klotz & Wolff, 1995; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003, also cf. Schmidt, Haberkamp, & Schmidt, 2011), which has not been applied in research on specific phobias before. In response priming, participants have to classify a target stimulus (e.g., a shape or color stimulus or a natural image of an animal) into two response categories (e.g., spider or snake), performing a speeded motor response. The target stimulus (e.g., a spider) is preceded by a prime stimulus triggering either the same response as the target (*consistent prime;* e.g., another spider) or the opposite response (*inconsistent prime;* e.g., a snake). If the prime is consistent, it speeds responses to the target; if it is inconsistent, it slows responses. This *response priming effect* increases with increasing stimulus-onset asynchrony (SOA) between prime and target for SOAs approximately up to 100 ms (Vorberg et al., 2003) and is defined as response time differences between consistent and inconsistent trials. While response compatibility paradigms have been used before to study processing advantages for fear-relevant material, response priming has special properties that have not yet been demonstrated for other paradigms. Firstly, many studies have confirmed that primes directly initiate the specific motor responses assigned to them, an effect clearly discernible in the time-course of lateralized readiness potentials and overt pointing movements (e.g., Leuthold & Kopp, 1998; Schmidt, 2002). Therefore, response priming effects are directly related to the visuomotor processes triggered by visual stimuli, and are sensitive to differences in visuomotor processing. Secondly, behavioral and electrophysiological evidence links response priming to visuomotor feedforward processing, because the earliest output of the motor system is controlled exclusively by the prime but is independent of all properties of the target. This was established for goal-directed pointing responses (Schmidt, Niehaus, & Nagel, 2006; Schmidt & Schmidt, 2009) as well as lateralized readiness potentials (Vath & Schmidt, 2007), just as expected from a simple feedforward system that processes prime and target in strict sequence. As far as we know, response priming effects are confined to two-choice responses, possibly because the underlying mechanism depends on a winner-takes-all process involving mutual inhibition of response alternatives (see Vorberg et al., 2003, for a model).[3]

We hypothesized that spider-fearful and snake-fearful participants will show enhanced visuomotor processing of spider or snake images, respectively, compared to neutral images and responses of a non-anxious control group, and that response priming effects can be used to measure this enhancement. We expected similar results for the two types of phobia (Åhs et al., 2009; Soares & Öhman, 1993). Based on our previous research on response priming, we predicted that enhanced processing of phobic primes will lead to larger response priming effects, and that enhanced processing of phobic targets will lead to faster overall response times. Because the perceptual learning account predicts that processing enhancements for fear-relevant stimuli should be apparent even in the fastest motor responses, we are especially interested in the earliest deciles of the response time distribution.

The present study

The experiment was designed as follows. Three groups of participants took part in the study; one group of spider-fearful participants with no fear of snakes, one group of snake-fearful participants with no fear of spiders, and one non-anxious control group with no fear of either spiders or snakes. The stimuli comprised four categories of natural images (spiders, snakes, mushrooms, and flowers). We decided to use natural images due to their high ecological validity. Spider pictures are *fear-relevant* to non-anxious and snake-fearful participants, but *phobic* to spider-fearful participants. Snake pictures are fear-relevant to non-anxious and spider-fearful participants, but phobic to snake-fearful participants. Mushrooms and flowers are assumed to be *neutral* for all three groups.

In each trial of the experiment, one prime and one target, chosen randomly from one of the four stimulus categories, were presented in rapid sequence, and participants performed speeded keypress responses to classify the targets into two response categories. Participants either had to discriminate spider and snake targets from mushroom and flower targets ("animal vs. non-animal" task) or spider and mushroom targets from snake and flower targets ("spider/mushroom vs. snake/flower" task) (Fig. 1).

We employed a within-subjects design where the same participants were observed throughout different conditions. This design allowed us to test all our crucial predictions by comparing different types of stimuli *within any participant group*, instead of the more traditional clinical design where different groups are compared to each other. As a result, statistical precision is greatly enhanced because the total error variance between participants can be removed from the tests (Stevens, 1996). This way, data patterns can be reliably observed in single participants, especially when a small group of individuals is observed over many repeated trials. Our participants completed six sessions with 960 trials per session, summing up to over 5,000 data points per individual. Each group had a size typical for a psychophysical response priming experiment. We consider that this approach allows us to detect small but consistent differences between stimulus conditions.

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[3] Note that "response priming" is the proper name of the paradigm, named so because of the ability of the prime to trigger a motor response. There is no assumption that effects are exclusively motoric, as opposed to visual, semantic, or other priming processes.

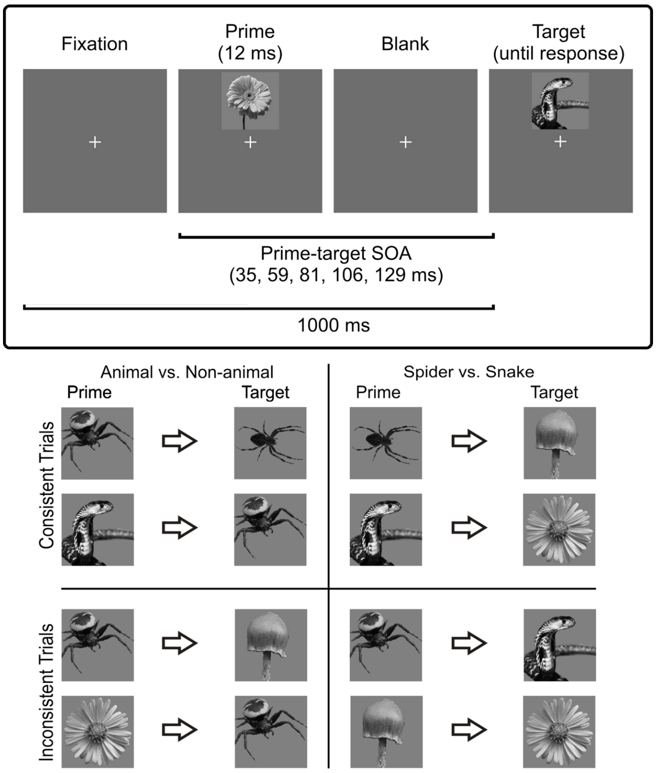

Figure 1. Stimuli and Procedure. Primes and targets were presented in the sequence displayed. Targets functioned as backward masks for preceding primes. In each trial, the prime was either consistent or inconsistent to the target with respect to the task-relevant motor response.

Methods

Participants. Twenty-six participants, mostly students from the University of Kaiserslautern, took part in the study. All of them were naïve to the purpose of the study. Eight of them reported that they were highly afraid of spiders but not of snakes (5 women and 3 men; age range, 20-30 years) and seven reported being highly afraid of snakes but not of spiders (5 women, 2 men; age range, 20-30 years). The remaining eight participants reported being afraid of neither spiders nor snakes (5 women, 3 men, age range, 17-24 years). All participants were screened for fear of spiders or snakes before the experiment started (Fig. 2). For this purpose, two spider questionnaires and one snake questionnaire were applied (German version of the “Spider Questionnaire” SPQ; Hamm, 2006; original version by Klorman, Weerts, Hastings, Melamed, & Lang, 1974; German questionnaire “Fragebogen zur Angst vor Spinnen” FAS; Rinck et al., 2002; German version of the “Snake Questionnaire” SNAQ; Hamm, 2006; original version by Klorman et al., 1974).

To ensure that the fear was specific to spiders or snakes, spider-fearful participants had to score above 75th percentile in the spider questionnaire and below 25th percentile in the snake questionnaire (and vice versa for snake-fearful participants). One participant fearful of spiders scored in the 33rd percentile of the fear-irrelevant snake questionnaire (SNAQ) but was included because of scores above 90th percentile in the SPQ. Two additional participants who reported being highly afraid of spiders were excluded after the diagnostic session due to high scores in the snake questionnaire. One additional participant who reported being highly afraid of snakes was excluded due to high scores in the spider questionnaires. These participants are already excluded from the number of participants mentioned above.

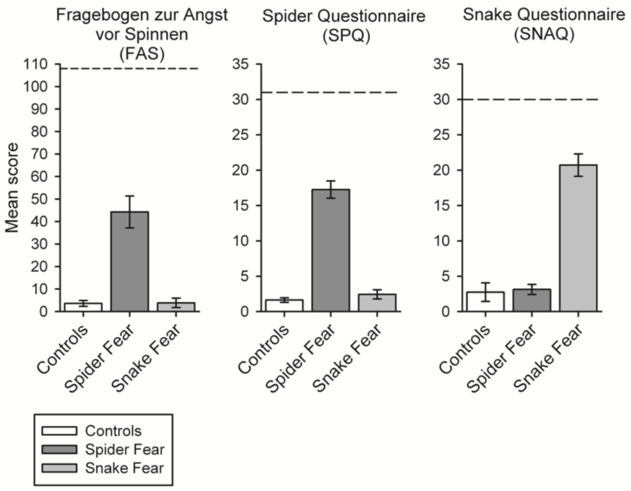

Figure 2. Results of two spider and one snake questionnaire (German version of the “Spider Questionnaire” SPQ; Hamm, 2006; German questionnaire “Fragebogen zur Angst vor Spinnen” FAS; Rinck et al., 2002; German version of the “Snake Questionnaire” SNAQ; Hamm, 2006) separately for three different groups (non-anxious controls, spider-fearful, and snake-fearful participants). Dashed lines indicate the maximum score obtainable in the respective questionnaire.

In addition, all spider- and snake-fearful participants completed the Beck Depression Inventory (BDI; Beck, Ward, Mendelson, Mock, & Erbaugh, 1961) and were tested for specific anxiety disorders using a structured diagnostic interview (“Diagnostic Interview for Psychological Symptoms (DIPS)”; Schneider

& Margraf, 2006), based on the DSM-IV-TR (APA, 2000). None of the participants were excluded for high depression scores on the BDI (mean = 6.67, sd = 5.98). All participants except one met at least four criteria for specific phobia. The criterion that was not satisfied in most cases (criterion E) states that the individual's fear, anxiety, or avoidance causes significant distress or significant interference in the person's day-to-day life. For this reason, we will refer to participants in the experimental groups as "fearful" instead of "phobic".

Participants had normal or corrected-to-normal visual acuity and received payment of € 8 per hour. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association.

Apparatus. The participants were seated in a dimly lit room in front of a color cathode-ray monitor (1280x1024 pixels, retrace rate 85 Hz) at a viewing distance of approximately 70 cm.

Stimuli and Procedure*.* Four different categories of grayscale images (spiders, snakes, mushrooms, and flowers), each containing thirty-five different pictures (4.16° of visual angle; 1 mm ≈ 0.008° of visual angle), were presented against a lighter gray background (8.75 cd/m^2). Each trial started with the appearance of the central fixation point (Fig. 1). After a varying delay, the prime was displayed for 12 ms either above or below the fixation point at 3.74°. Subsequently, the target was presented at the same position at prime-target SOAs of 35, 58, 81, 105, or 128 ms and remained on screen until the participant's response. In each trial, the prime was either consistent or inconsistent with the target with respect to the required motor response. Prime and target pictures were pseudo-randomly drawn from one of the four different categories and a data base of thirty-five pictures for each category. All stimulus combinations of prime and target picture categories and prime-target SOA occurred equiprobably and pseudo-randomly in a repeated-measures design.

We employed two speeded target classification tasks: All participants either discriminated spiders and snakes from flowers and mushrooms *("animal vs. non-animal" task)* or spiders and mushrooms from snakes and flowers *("spider/mushroom vs. snake/flower" task)* (Fig. 1). In the "animal vs. non-animal" task, participants categorized the targets as quickly as possible by pressing the left button for snakes and spiders and the right button for flowers and mushrooms (or vice versa). In the "spider/mushroom vs. snake/flower" task, participants pressed the left button for spiders and mushrooms and the right button for snakes and flowers (or vice versa). This contrast is essential to separate real processing advantages for phobic material from mere response biases. For instance, in the "animal vs. non-animal" task, a generalization effect from spider to snake pictures might emerge because the two unpleasant image categories are matched to the same response. The "spider/mushroom vs. snake/flower" task controls for that effect. Note that we grouped spider with mushroom pictures in that task because of the visual similarity of flowers and spiders, to limit effects of simple shape priming in our results. In any task, primes and targets were classified as "consistent" when mapped to the same response, and "inconsistent" when mapped to opposite responses.

Each participant performed both tasks in separate sessions; the assignment of left and right response keys was counterbalanced across participants. Participants received immediate auditory feedback on correctness of their response after each trial. Each participant performed three 1-hour sessions performing the "animal vs. non-animal" task and three 1-hour sessions performing the "spider/mushroom vs. snake/flower" task, with order counterbalanced across participants. Each session started with one practice block followed by 29 blocks of 32 trials. Participants were debriefed after the final session and received an explanation of the experiment.

At the end of the final session, participants were asked to evaluate the images applied in the study. The rating involved three dimensions (valence, arousal, and disgust). All dimensions were rated on a six-point rating scale. Scales were coded so that high scores reflected high arousal and disgust, respectively. Positive scores in the valence ratings represent positive emotions towards the image, a score of zero means that neither positive nor negative emotions are involved, and negative scores reflect negative emotions (for results see Table 1). All three scores were submitted as dependent variables to multivariate analysis of variance with factors of group and image category. In the image rating, the groups (non-anxious controls, participants afraid of spiders, participants afraid of snakes) differed significantly regarding their evaluations. As expected, a main effect of group (Wilk's $\Lambda = 0.60$, $F(6, 156) = 7.46$, $p < .001$) and picture category ($\Lambda = 0.18$, $F(9, 189.98) = 21.73$, $p < .001$), as well as an interaction effect of group and picture category was found ($\Lambda = 0.21$, $F(18, 221.10) = 9.15$, $p < .001$), reflecting the fact that fearful participants rated their phobic images more negatively on all three dimensions as compared to neutral images or non-fearful participants. Note that the group of spider- and snake-fearful participants rated the picture categories of their specific fear comparably over all three dimensions (High spider fear: Arousal: 3.12, Disgust: 4.26, Valence: -2.55; High snake fear: Arousal: 3.45, Disgust: 4.31, Valence: -2.30). Therefore, we conclude that the phobic images induce similar amounts of discomfort in spider- and snake-fearful participants.

Data treatment and statistical methods. Practice blocks were not analyzed. Trials were eliminated if response times were shorter than 100 ms or longer than 1000 ms, and if, incidentally, prime and target consisted of the exact same image. These criteria eliminated 1.51 % of trials in the “animal vs. non-animal” task and 1.79 % of trials in the “spider/mushroom vs. snake/flower” task. Repeated-measures analyses of variance (ANOVAs) were performed with Greenhouse-Geisser-corrected p values. We report F values with subscripts indicating the respective effect (e.g., F_{CxS} for the interaction of consistency and SOA). Additionally, we report the effect size η^2 (cf. Levine & Hullett, 2002).

Results

The large number of conditions in this experiment requires a principled way of analyzing the data. We organized the results section according to a robust empirical principle in response priming, namely, that the strength of the target stimulus mainly affects total response times, while the strength of the prime mainly affects the size of the priming effect. The results section will be structured as follows. Within each of the three groups (spider-fearful, snake-fearful, control), we will first analyze the *influence of the different targets on overall response times* as a measure of response activation by the different targets (spider, snakes, mushrooms, flowers). Second, we will examine the *influence of the different primes on response priming effects* as a measure of response activation by the primes. Finally, we will show that the effects found in the general response times are already present in the fastest responses (deciles 2nd and 3rd). (The 1st percentile is not well suited for such an

Table 1. Participants’ mean scores (with standard deviations) for image evaluation separately for scale (valence, arousal, and disgust) for each picture category and each group. Bold letters indicate phobic image categories.

	Arousal				Disgust				Valence			
	Spider	Snake	Mushroom	Flower	Spider	Snake	Mushroom	Flower	Spider	Snake	Mushroom	Flower
Controls	0.61 (0.86)	0.67 (1.00)	0.39 (0.65)	0.58 (0.89)	0.98 (1.17)	0.23 (0.61)	0.43 (0.73)	0.04 (0.19)	-0.40 (1.07)	0.00 (0.92)	-0.27 (1.01)	0.35 (1.02)
High spider Fear	**3.12 (1.31)**	0.66 (0.92)	0.17 (0.47)	0.06 (0.23)	**4.26 (1.38)**	0.69 (0.92)	0.34 (0.90)	0.01 (0.10)	**-2.55 (0.74)**	-0.15 (0.87)	-0.15 (0.53)	1.04 (0.94)
High snake Fear	1.01 (1.11)	**3.45 (1.46)**	0.11 (.034)	0.10 (0.38)	1.01 (1.11)	**4.31 (1.43)**	0.16 (0.57)	0.01 (0.11)	-0.61 (0.84)	**-2.30 (0.71)**	-0.07 (1.00)	1.18 (1.32)

analysis because it is too dependent on the exact outlier criteria.)

Influence of the targets on overall response times. In this analysis, we look at overall response time (averaged across consistent and inconsistent primes) as a measure of response activation by the target. Because we found no significant interactions of the task factor with any of the other factors, we averaged the response times for both tasks (Fig. 3, upper plot). We performed an analysis of variances (ANOVA) with factors of group *(G)*, target category (*T;* spider, snake, mushroom, flower), prime-target consistency (*C;* consistent, inconsistent), and SOA (*S;* 35, 58, 81, 105, 128 ms). However, because consistency and SOA effects are not of theoretical interest in this particular analysis, we do not report them here. The test on the interaction of group and target was significant, $F_{GXT}(6, 60) = 5.45$, $p = .001$, $\eta^2 = 0.179$, confirming our prediction that target effects differed systematically between groups.

Additionally, we performed an analysis of variance (ANOVA) for each group. We had predicted that participants fearful of spiders or snakes should respond faster to their respective phobic targets than to any other target category, while no such processing preference should occur in the non-anxious control group. Indeed, in the control group, participants responded equally fast to all types of targets ($F_T(3, 21) = .87$, $p = .428$, $\eta^2 = 0.010$; Fig. 3). In spider-fearful individuals, however, target category strongly influenced response times, mainly because responses were much faster when the target was a spider ($F_T(3, 21) = 12.71$, $p = .005$, $\eta^2 = 0.195$). Planned paired comparisons between the phobic targets and the remaining target categories confirmed significant differences for each contrast (*spider vs. snake:* $F_T(1, 7) = 16.47$, $p = .005$; *spider vs. mushroom:* $F_T(1, 7) = 20.21$, $p = .015$; *spider vs. flower:* $F_T(1, 7) = 14.52$, $p = .007$). In fact, response times to spider targets were about 43 ms faster compared to other targets. For participants fearful of snakes, responses to snake targets also were numerically faster, but not significantly so ($F_T(3, 18) = 2.95$, $p = .115$, $\eta^2 = 0.091$). Also, paired comparisons did not reveal significant differences between target types (snake vs. spider: $F_T(1, 6) = 0.62$, $p = .460$; snake vs. mushroom: $F_T(1, 6) = 4.17$, $p = .087$; snake vs. flower: $F_T(1, 6) = 5.87$, $p = .052$). Note, however, that the differences between snake targets and flower and mushroom targets approached significance.

Faster responses to phobic targets did not result from a speed-accuracy trade-off, as shown in Figure 3 (lower panel). In particular, spider-fearful participants responded not only faster but also more accurately when the target was a spider, and responses to phobic targets were also more resistant to priming effects.

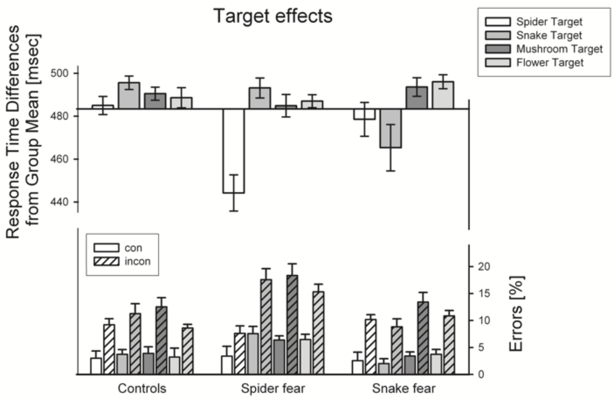

Figure 3. Upper panel: Response times to different target types averaged over both tasks for each group, shown relative to the grand average response time. Lower panel: Error rates (in percentage) are displayed separately for consistent trials (plain bars) and inconsistent trials (patterned bars). In both plots, different grey scales indicate different target types. Here and in all remaining figures, error bars denote standard errors of the mean with pure intersubject variance removed (Cousineau, 2005).

Influence of the primes on priming effects. In this analysis, we looked at response priming effects (defined as response time differences between consistent and inconsistent trials) as a measure of response activation by the primes. For each group, we performed an ANOVA with factors of prime (*P*; spider, snake, mushroom, flower), consistency *(C),* and SOA *(S)*. We predicted that participants fearful of spiders or snakes should show larger priming effects by their respective phobic primes than by any other prime category, while no such processing preference should occur in the non-anxious control group.

Response times for the different groups and prime types in the two tasks are displayed in Figure 4. Averaged across prime type, consistent trials (where prime and target stimuli belonged to the same response category) produced faster response times than inconsistent trials for each group and task ("animal vs. non-animal", "spider/mushroom vs. snake/flower", respectively; *controls*: $F_C(1, 7) = 63.26$, and 95.00, both $p < .001$, $\eta^2 = 0.222$ and $\eta^2 = 0.366$; *high spider fear*: $F_C(1, 7) = 163.96$, and 189.96, both $p < .001$, $\eta^2 = 0.268$ and $\eta^2 = 0.204$; *high snake fear*: $F_C(1, 6) = 92.95$, and 74.02, both $p < .001$, $\eta^2 = 0.284$ and $\eta^2 = 0.224$). Also, priming effects increased with prime-target SOA for all groups and tasks (*controls*: $F_{CxS}(4, 28) = 12.02$, and 13.65, $p = .001$ and $p < .001$, $\eta^2 = 0.016$ and $\eta^2 = 0.038$; *high spider fear*: $F_{CxS}(4, 28) = 25.13$, and 17.67, both $p < .001$, $\eta^2 = 0.032$ and $\eta^2 = 0.022$; *high snake fear*: $F_{CxS}(4, 24) = 20.35$, and 18.06, both $p < .001$, $\eta^2 = 0.025$ and $\eta^2 = 0.030$).

Response priming effects can be observed in error rates as well as response times. Because consistent primes activate only correct responses whereas inconsistent primes activate only incorrect responses, errors should be observed predominantly in inconsistent trials at long SOAs where the primes have had a lot of time to drive the incorrect response (Vorberg et al., 2003). Figure 4 shows that priming effects in error rates closely follow those in the response times. In particular, participants fearful of spiders show large error rates when the target is preceded by a response-inconsistent spider prime. No such effect is discernible in the snake-fearful participants, in accordance with the pattern in the response times.

In the following, we report the results separately for each task, for the four different prime types, and for each group, and highlight

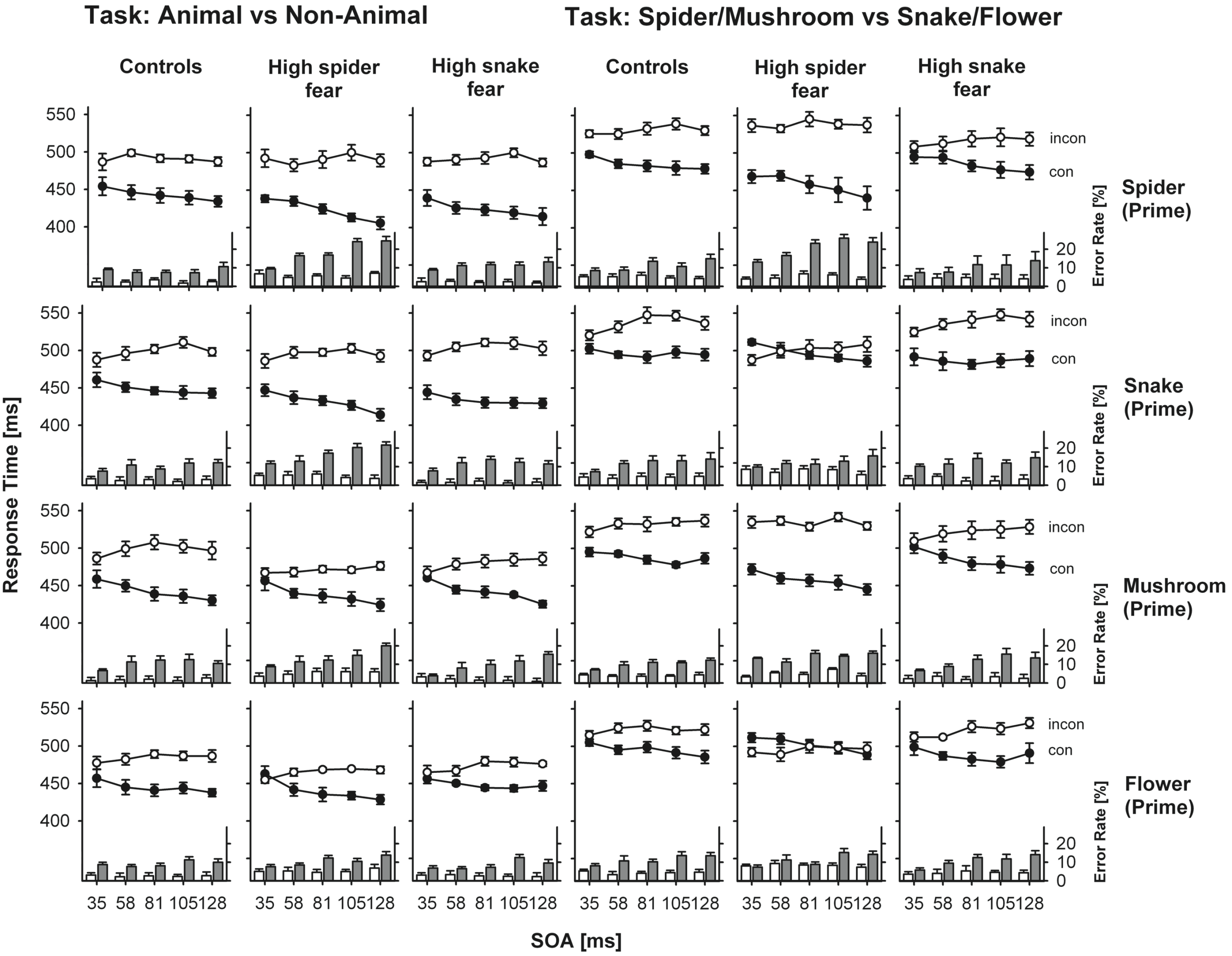

Figure 4. Response times and error rates in each task and group, separately for different prime types.

the differences between the control and the two experimental groups.

“Animal vs. non-animal” task. An ANOVA with factors of group *(G)*, prime (*P*; spider, snake, mushroom, flower), consistency *(C),* and SOA *(S)* yielded no significant interactions of the group factor with either prime type or priming effect ($F_{GxP}(6, 60) = 1.90$, $p = .116$, $h^2 = 0.079$; $F_{GxPxC}(6, 60) = 1.72$, $p = .196$, $h^2 = 0.102$).

“Spider/mushroom vs. snake/flower” task. In the previous task, spider and snake stimuli were always mapped to the same motor response. If participants developed a bias against the response assigned to the phobic stimuli (e.g., the spiders), this bias would translate to the other animal category as well (i.e., the snakes), and differences between phobic and merely fear-relevant stimuli could not be interpreted. The “spider/mushroom vs. snake/flower” task allows us to compare phobic and merely fear-relevant primes in a situation where they are mapped to different responses. We predict faster overall response times to phobic targets as compared to other target categories, larger priming effects by phobic primes as compared to other prime categories, and no such effects of stimulus type in the control group. An ANOVA with factors of group *(G)*, prime (*P*; spider, snake, mushroom, flower), consistency *(C),* and SOA *(S)* revealed that response times to the four different prime types varied significantly across groups, $F_{GxP}(6, 60) = 3.90$, $p = .006$, $h^2 = 0.169$, and that the priming effects elicited by those prime types also differed across groups, $F_{GxPxC}(6, 60) = 5.18$, $p = .010$, $h^2 = 0.285$.

As expected, non-anxious control participants showed no differences in priming effects for the four different prime categories ($F_{PxC}(3, 21) = 2.56$, $p = .135$, $h^2 = 0.020$) or the two different prime response classes (spiders and mushrooms forming one class, spiders and flowers the other; $F_{PxC}(1, 7) = 2.05$, $p = .195$, $h^2 = 0.012$). In contrast, in spider-fearful participants priming effects differed significantly for the four different prime categories ($F_{PxC}(3, 21) = 11.64$, $p = .007$, $h^2 = 0.194$) as well as for the two different prime response classes ($F_{PxC}(1, 7) = 13.42$, $p = .008$, $h^2 = 0.196$). However, no significant differences in priming effects were found for participants specifically fearful of snakes (four primes: $F_{PxC}(3, 18) = .34$, $p = .599$, $h^2 = 0.010$; two prime response classes: $F_{PxC}(1, 6) = 1.04$, $p = .347$, $h^2 = 0.002$). For further understanding of that pattern, we separated response times in the two groups by both prime and target category (Fig. 5). This analysis reveals that priming effects are difficult to evaluate without taking the main effects of target type into account. Specifically, responses to phobic targets (spiders for spider-fearful, snakes for snake-fearful participants) were relatively faster than those to neutral targets (mushrooms or flowers). For instance, when spider-fearful participants responded to phobic spider targets, their responses were fast even if these targets followed an inconsistent prime. As a result, priming effects are *augmented* when a fast phobic target is response-consistent with the prime, because then the response to the consistent target is speeded both by the priming effect and by the main effect of target type. Similarly, priming effects are *reduced* or even appear to vanish when a phobic target appears in the response-inconsistent role, because then the response is slowed by the priming effect but still speeded by the main effect of the target. This augmentation-reduction pattern is especially pronounced in the spider-fearful group when responding to spider targets; it is less apparent for the snake-fearful group when responding to snake targets (cf. Fig. 4). This is of course a consequence of the larger target main effects in the spider-fearful group.

In sum,, the response pattern in the “spider/mushroom vs. snake/flower” task is similar to the “animal vs. non-animal” task, indicating that any differences between phobic and merely fear-relevant images cannot be attributed to the fact that they are both assigned to the same response category. However, it is noteworthy that participants responded up to 43 ms slower in the “spider/mushroom vs. snake/flower” than in the “animal vs. non-animal” task. This might be due to higher demands in the former task. Specifically, in the “animal vs. non-animal” task, the response categories are consistent with an intuitive, natural classification of the environment, whereas in the “spider/mushroom vs. snake/flower” task, participants had to learn a purely arbitrary assignment.

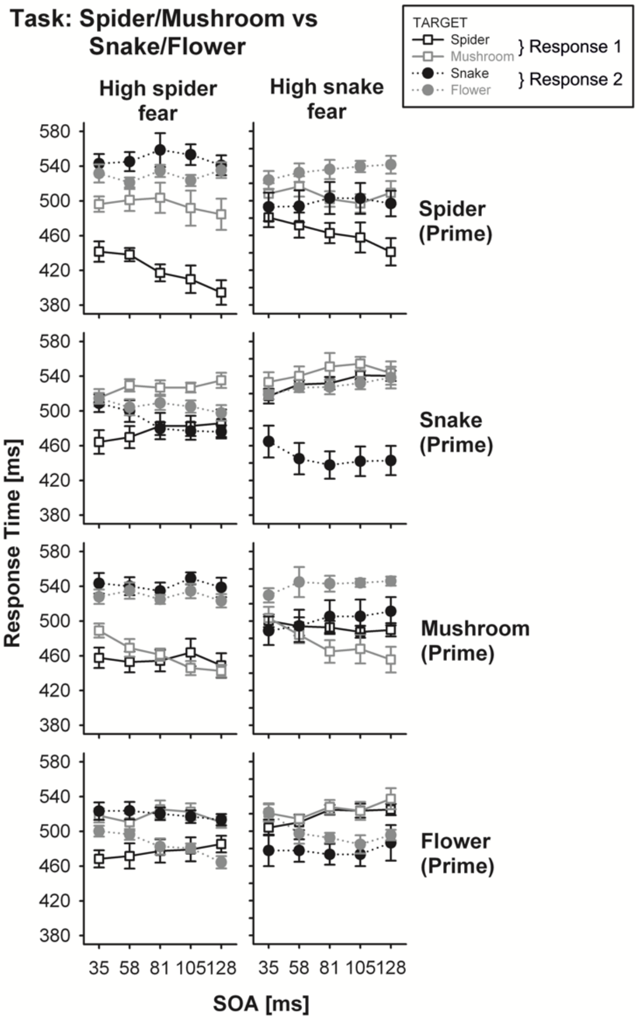

Figure 5. Response times of spider and snake fearful individuals in the “spider/mushroom vs. snake/flower” task, separately for different prime and target types.

Results of 2nd and 3rd deciles. If the processing advantage for fear-relevant material is due to long-term perceptual learning processes, the advantage could already affect the first sweep of processing running through the visuomotor system. If so, processing advantages should be fully present in the fastest responses (Schmidt et al., 2011). This is true for the effect of phobic targets on overall response time (Fig. 6; cf. Fig. 3) as well as for the effect of phobic primes on the magnitude of the priming effect (Fig. 7). There is no indication in our data that these effects become any larger with increasing response time.

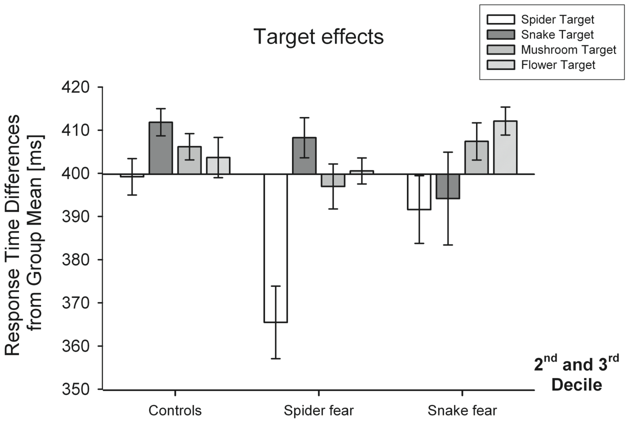

Figure 6. Response times to different targets averaged over both tasks for each group, shown relative to the grand average response time for 2nd and 3rd deciles of the response time distribution.

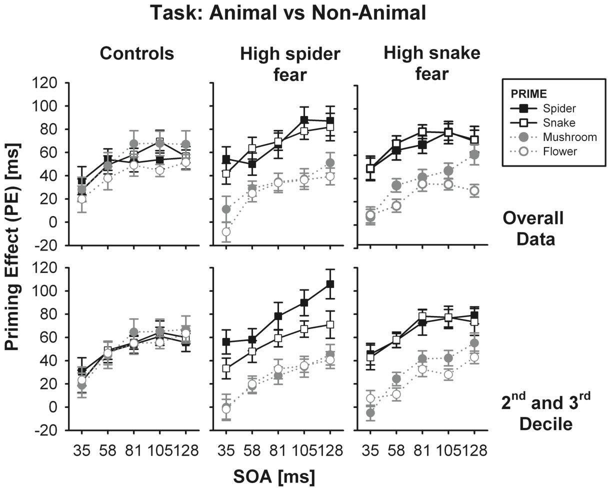

Figure 7. Priming effects (PE) in overall response times (upper row) compared to PEs in the 2nd and 3rd deciles (lower row) for the “animal vs. non-animal” task.

Discussion

The present results

Overall, we found robust response priming effects in all groups and tasks, where inconsistent primes led to slower response times compared to consistent ones, and these priming effects increased with prime-target SOA (complications to this overall data pattern are discussed below). These findings are in line with previous results from the image classification literature (e.g., Bacon-Macé, Kirchner, Fabre-Thorpe, & Thorpe, 2007; Kirchner & Thorpe, 2006) as well as response priming studies with natural images (Schmidt & Schmidt, 2009), showing that natural images are able to rapidly activate the motor responses assigned to them.

The purpose of the present study was to utilize such response priming effects to demonstrate enhanced visuomotor processing of phobic stimuli relative to merely fear-relevant and neutral stimuli, and to investigate whether such processing advantages might conceivably be due to enhanced feedforward processing of visual stimuli. Of special interest in the present study are systematic differences in the processing of different image categories within each group of spider-fearful, snake-fearful, and non-anxious control participants. In response priming studies, such differences should show up in the overall response times (reflecting processing aspects of the target) as well as in the magnitude of priming effects (reflecting processing aspects of the prime).

In the control participants, we found no systematic differences in their responses towards the different target categories (spiders, snakes, mushrooms, or flowers), neither in the “animal vs. non-animal” nor in the “spider/mushroom vs. snake/flower” task. Also, all primes produced strong and reliable priming effects whose magnitudes did not differ for the different prime categories. We had been prepared to find processing advantages for fear-relevant images in accordance to recent findings (e.g., Anderson & Phelps, 2001; Öhman et al., 2001; Piech et al., 2010), at least in the “animal vs. non-animal” task. In that task, the simple categorization of animal vs. non-animal targets is known to lead to fast classification responses, so that mapping spider and snake images to the same response might reveal a processing difference between fear-relevant and neutral stimuli even in control participants. The absence of such differences in our study is consistent with the fact that control participants rated the images of spiders and snakes as only slightly negative, arousing, or disgusting (Table 1). Similarly, Tipples and colleagues (2002) did not find any biases for threatening stimuli in non-anxious individuals in a visual search task. The conflicting findings suggest that non-anxious control participants in various studies may differ in research-relevant characteristics, such as their trait/state anxiety (see, e.g., Koster, Verschuere, Crombez, & Van Damme, 2005; Mogg, Bradley, Miles, & Dixon, 2004). One could argue that the observed differences in the presented images are due to differences in low level vision. However, as one reviewer pointed out the results of the non-anxious control group demonstrate comparable processing efficiency for all different image types.

Importantly, spider-fearful participants showed a strongly different result pattern.[4] Firstly, they responded more rapidly to spider targets as compared to snake, mushroom, and flower targets. Secondly, their responses to spider targets were exceptionally fast even in cases where these targets followed an inconsistent prime. The fast responses to spider targets strongly affected the size of the priming effect. This can most clearly be seen in the “spider/mushroom vs. snake/flower” task. For instance, if the prime was a spider, a subsequent spider target led to exceptionally large priming effects because fast responses to the spider target became even faster by consistent priming. In contrast, when the prime was a snake, priming effects were reduced because responses to the spider target were still relatively fast, even though the target was inconsistent to the prime. As a result, priming

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[4] Note that we were able to replicate these findings with a similar design in the spider-fearful group in a follow-up study. Snake-fearful participants did not participate in that experiment.

effects are augmented if spider targets appear in consistent conditions and are diminished if they appear in inconsistent conditions. Taking this complication into account, our results clearly show that spider targets and spider primes lead to faster responses and larger priming effects, respectively, in participants fearful of spiders, compared to other image categories.

Unexpectedly, snake-fearful participants showed a response pattern different from that in the spider-fearful group. In comparison to responses to neutral images, they tended to respond somewhat faster not only to snake targets, but also to spider targets. However, neither effect was significant, so it has to be concluded that information processing was not specifically accelerated by snake pictures. In the “animal vs. non-animal” task, priming effects were significantly larger when an animal prime was shown compared to trials when non-animal primes were presented, but again, there were no discernible differences between snake and spider primes. Furthermore, even though response times to animal targets were faster than those to non-animal targets, the faster responses occurred indiscriminately within the category of animal pictures, that is, snake-fearful participants did not respond specifically faster to their phobic picture category. Thus, it seems that they show enhanced information processing not limited to snake pictures, but to fear-relevant animal stimuli in general. However, some care is needed when interpreting these group differences, since this is an accidental finding not previously reported in the literature and our experiment is designed to pick up differences between stimuli within groups rather than differences between groups.

The major reason for applying two tasks with different stimulus-response mappings was to control for generalization effects, i.e., effects in response times to snake targets emerging solely because spiders and snakes are matched to the same motor response. The “spider/mushroom vs. snake/flower” task controls for such effects. In the present results, however, response time effects in all groups can be traced back to the specific image category presented as prime or target. In other words, no generalization effects are apparent in the present study, so that both tasks seem suited for measuring enhancements in response activation. The comparison of the two tasks also tells us something about the type of information on which the response priming effect is based. In the “animal vs. non-animal” task, several types of information may conspire to prime a response: the semantic information about the animacy of primes and targets, the affective information about the pleasantness of fear-relevant vs. neutral image categories, and the stimulus-response mapping assigned at the outset of the experiment. In contrast, the “spider/mushroom vs. snake/flower” task makes stimulus-response assignments orthogonal to the animacy and pleasantness distinctions, leaving only the visuomotor mapping as a source of priming information. As similar priming effects and processing enhancements are observed in both tasks, we can exclude semantic as well as affective information as *exclusive* sources of priming. Otherwise, neutral pictures of mushrooms and flowers would not have been able to prime fear-relevant pictures of spiders and primes (and vice versa), which is what we found in the “spider/mushroom vs. snake/flower” task (Fig 5). On that note, we also can preclude pure identity priming because responses are always activated by both types of stimuli that are assigned to it.

Underlying mechanisms of rapid information processing

As described in the introduction, two different accounts attempt to explain enhanced information processing by threatening stimuli: acceleration due to increased *amygdala activation* and *long-term perceptual learning* mechanisms. The perceptual learning account with respect to enhanced object recognition can easily explain why enhanced processing of phobic stimuli is evident in the fastest responses of the response time distribution. In object recognition, elementary features (e.g. color, form) must be bound into objects; for example, eight black pins and one black oval body may be bound into the silhouette of a spider. According to many authors, this process requires attentional resources and should therefore be time-consuming (e.g., Treisman, 1996; Roelfsema, 2006). Contradicting this view, VanRullen (2009) pointed out that this is in conflict with the remarkable speed of object categorization responses in natural scenes. He therefore suggests the possibility of ‘hardwired’ binding of features to which a person is frequently exposed (i.e., perceptual learning). For example, if a person is frequently exposed to spiders, this might induce enhancements in the functional properties of the cortical arrays involved in spider detection and recognition. If the person also perceives spiders as threatening, this process might be additionally strengthened by attentional biases. Thus, perceptual learning modulates the processing hardware concerned with that stimulus class, and so the processing advantage encompasses the first feedforward sweep of visual processing. We argue for a feedforward theory of response priming, suggesting that it is based on sequential feedforward sweeps elicited by prime and target stimuli which activate the associated motor responses in strict sequence and without temporal overlap (*rapid-chase theory;* Schmidt et al., 2006; Schmidt et al., 2011). This theory predicts that the motor response should first be controlled exclusively by the prime signal and only later by the actual target signal. Because the theory assumes that the target’s feedforward sweep cannot catch up with that of the prime, it makes the strong prediction that response priming effects should be fully present in the fastest responses and not increase any further for longer response times. Indeed, in the present data all modulatory effects of phobic material on response times and priming effects were fully present in the fastest responses, that is, the 2nd and 3rd deciles of the response time distribution, consistent with such a simple feedforward model. Note that the perceptual learning account could also accommodate differential enhancement for different phobias. For instance, because the likelihood of encountering a snake is low for German participants compared to the likelihood of encountering a spider, our snake-fearful participants may have had less opportunity for perceptual learning than the spider-fearful participants, and less incentive for continued vigilance in interactions with their everyday environment. However, since our study was not designed to investigate group rather than stimulus differences, this suggestion is somewhat speculative at this point.[5]

Our finding that the processing advantage of phobic stimuli already affects the fastest responses places serious time constraints on any explanation involving the amygdala, especially considering the processing speed of the structures involved (cf. Piech et al., 2010; Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009). If images can indeed be classified during the first feedforward sweep of visuomotor processing (Schmidt & Schmidt, 2009; Thorpe et al., 1996; VanRullen & Thorpe, 2001), the amygdalar pathway would be required to (1) classify objects as emotionally relevant, (2) outpace the cortical object recognition route, and (3) exert modulatory control on that processing route before it finishes processing the object. It is questionable whether all these processes can take place in the minimal time available in the rapid categorization task that we used, considering that all amygdalar modulation of the object-recognition pathway must be finished before the fastest responses are completed. Mormann et al. (2011) analyzed response latencies from single neurons in the amygdala and found that they responded to animal pictures within 324 ms, significantly faster than to other image categories. The authors argue that this enhancement may reflect the biological importance of animal pictures, but stress that “the observed amygdala latencies are nevertheless similar to those found in other regions in the temporal lobe, and thus seem more likely to be generated along the cortical object recognition pathway than via a rapid subcortical route” (p. 1248). Note that the amygdala’s response time reported by Mormann et al. is already close to the fastest keypress responses to

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[5] Note, however, the interesting prediction that individuals fearful of spiders *as well as* snakes should show a response pattern similar to those of the spider-fearful participants and, at the same time, should show no enhanced processing of snake pictures. This is exactly what we found in the three participants who were excluded from the main analyses because they scored high in both the spider and snake and snake questionnaires. However, these findings have to be interpreted with caution due to the very small sample size.

spider targets in our study, which average about 365 ms in the 2nd and 3rd decile of the response time distribution. Moreover, the time when the keypress response is completed is preceded by a phase of motor preparation that takes about 100 ms and can be traced, for instance, in lateralized readiness potentials (cf. Vath & Schmidt, 2007). Thus, when these timing issues are considered together, the amygdala seems just too slow to modulate visuomotor processing of primes or targets in an on-line fashion (see also Pessoa & Adolphs, 2010). It may, however, be crucial for the emotional response experienced after or simultaneously with the ongoing motor response.

In addition, if enhanced processing were due to an *emotional* response at all, one would expect the enhancement to be predictable from the emotional evaluation of the stimulus. Spider-fearful and snake-fearful participants in our study gave comparable ratings to their feared stimuli, respectively, yet strong processing enhancements for phobic material only occurred in spider-fearful participants, while snake-fearfuls showed only slight enhancements for both types of animal stimuli. Of course we did not measure amygdala activation directly and have to infer it from the self-reported fear levels; so we cannot rule out that amygdala activation might differ across experimental groups. But even if the processing enhancement was indeed based on a signal by the amygdala, this response would be required to occur freshly for each stimulus presentation, without much fatigue or adaptation, over the course of several thousand trials. All this suggests that emotional activation by the amygdala may not play a causal role in speeding perceptual processing on-line, that is, on a trial-to-trial basis. In the long run, however, emotional responses directed by the amygdala may play an important role in promoting long-term perceptual learning.

In summary, our results show that phobic stimuli are processed faster in the visuomotor system as compared to merely fear-relevant or neutral ones, as revealed by differences in response times and response priming effects. This processing advantage is fully present in the fastest motor responses but may occur only in spider-fearful but not snake-fearful individuals. These findings support the notion that long-term perceptual learning processes underlie the automatic and rapid information processing of threatening images, and conflicts with the idea that the amygdala is involved in the online enhancement of these processes.

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