

Conscious awareness is required for the perceptual discrimination of threatening animal stimuli: A visual masking and continuous flash suppression study.

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Abstract

We investigated if the subliminal processing of threatening animal (snakes and spiders) and neutral object (cars and houses) stimuli can influence the discrimination of a subsequent visible stimulus. The prime and target pair were either identical, of the same category but with different physical features, or different in category and physical features. In two experiments, participants discriminated the basic level category (e.g. snake vs. spider) of a visible target stimulus that had been preceded by a visible or perceptually invisible prime stimulus. One experiment used visual masking to render prime stimuli perceptually invisible and the other used continuous flash suppression (CFS). Priming effects were demonstrated in both experiments when the prime was visible but not when the prime was rendered perceptually invisible. These findings demonstrate that conscious awareness could be required in the perceptual discrimination of threatening animal and neutral object images at their specific basic level category.

1. Introduction

From an evolutionary perspective, the rapid visual processing of threatening animals and other dangers serves a highly adaptive purpose for humans (Öhman, 2009). Studies demonstrate that this processing can occur outside of conscious awareness. For example, physiological responses, such as enhanced skin conductance (Öhman, 2009; Ruiz-Padial, Mata, Rodríguez, Fernández, & Vila, 2005; Tan, Li, Wang, & Yang, 2013) and neural activation (Carlsson et al., 2004; Fang, Li, Chen, & Yang, 2016), have been reported to occur in response to subliminally presented snakes and spiders. The subliminal presentation of a stimulus occurs when its bottom-up signals are either interrupted or insufficiently strong to cross the threshold necessary for conscious perception (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). It is not fully understood if this change in skin conductance and neural activation reflects the subconscious detection of a potentially dangerous stimulus, or the recognition and identification of the presented animal. Thus, we aimed to determine whether or not sufficient processing of information can take place during the subliminal presentation of a threatening animal to facilitate its identification in a subsequent visible presentation.

Visual masking and continuous flash suppression (CFS) are two techniques for presenting stimuli subliminally (for review, see Kim & Blake, 2005; Breitmeyer, 2015). Visual masking involves briefly presenting an image consisting of high-contrast noise 30 to 200 ms before and / or after a target (Breitmeyer & Ögmen, 2006) while CFS is an interocular technique in which a series of flashing high-contrast images, such as Mondrians, are displayed to one eye and a low-contrast target is displayed to the other (Tsuchiya & Koch, 2005). In both cases, the masks are perceptually seen while the target appears invisible. However, discrepancies in the literature have raised the concern that the two suppression techniques might lead to different residual neural processing and behavioural responses (Almeida, Mahon, Nakayama, & Caramazza, 2008; Almeida, Pajtas, Mahon, Nakayama, & Caramazza, 2013; Fogelson, Kohler, Miller, Granger, & Tse, 2014).

Often, the two suppression techniques are used during a priming paradigm (Van den Bussche, Van den Noortgate, & Reynvoet, 2009). In this context, a visible target is preceded by a prime that has been rendered perceptually invisible by means of either visual masking or CFS (Kouider & Faivre, 2017). The subconscious processing of the prime is inferred when it is able to influence the response to the subsequent target (Kiefer et al., 2011). In behavioural studies, this is evidenced by a decrease in reaction time and response error when the prime shares a common feature with the target (congruent prime) or by an increase in reaction time and response error when the prime does not (incongruent prime). Manipulating similarities and differences between the prime and target in either a visual masking or CFS experiment can provide insight into what can and cannot be processed subliminally (Kiefer et al., 2011).

Much debated is the extent to which subliminal priming reflects the processing of physical features (perceptual processing) or conceptual meaning (semantic processing) (Kouider & Dehaene, 2007). Studies have suggested that semantic and evaluative information such as valence can be extracted from a subliminally presented prime (Dell'Acqua & Grainger, 1999; Dehaene and Naccache, 2001; Draine & Greenwald, 1998; Greenwald, Draine, & Abrams, 1996; Pohl, Kiesel, Kunde, & Hoffman, 2010; Wentura & Degner, 2010). For example, Dehaene and Naccache (2001) demonstrated repetition priming effects for words along similar semantic categories, independent of whether the prime and target stimuli shared the same or different case (e.g. radio-RADIO). However, it is possible that Dehaene and Naccache (2001) did not fully suppress the perceptual visibility of their primes. Some authors have suggested that semantic processing can be present when participants are partially aware of the prime and that true subliminal priming is restricted to perceptual processing (e.g. Kouider

& Dupoux, 2004). Others have argued that the subliminal priming of words reflects automatically triggered response tendencies rather than the spreading activation in a semantic network (Abrams & Greenwald, 2000; Damian, 2001; Klinger, Burton, & Pitts, 2000). Manipulating the amount of overlapping perceptual and semantic information between a prime and a target using pictures could yield further insight into perceptual and semantic computations outside of conscious awareness – provided that the primes are properly rendered perceptually invisible.

Under visible conditions, Chouinard, Morrissey, Köhler, and Goodale (2008) presented prime-target image pairs that were either: 1) the same exemplar of an object (i.e. the same object twice) in which the physical and semantic features were identical between the two stimuli, 2) different exemplars of the same object (e.g. an open versus closed umbrella) in which the physical but not semantic features differed between the two stimuli, or 3) completely different objects in which both the physical and semantic features differed between the two stimuli. When participants named the target stimulus, priming was fastest for same exemplars, slower for different exemplars, and slowest for completely different objects – demonstrating both perceptual and semantic priming effects. The question arises as to whether or not similar results can be obtained when the prime is presented subliminally.

It is generally accepted that the amygdala plays a key role in processing emotional stimuli and is critically implicated in physiological arousal as measured by enhanced skin conductance (Tan et al., 2013) to stimuli associated with fear (Costafreda, Brammer, David, & Fu, 2008). Neuroimaging studies have demonstrated evidence for amygdala responsiveness to subliminal images of threatening animals (Carlsson et al., 2004; Fang et al., 2016). For example, a positron emission tomography (PET) study by Carlsson et al. (2004) found strong amygdala activation during the subliminal presentation of both phobic (e.g. snake image for snake phobic participants) and fear-relevant stimuli (e.g. snake image for spider phobic participants). In contrast, when stimuli were perceptually visible, strong amygdala activation was found for phobogenic stimuli, but not for fear-relevant, potentially due to inhibitory control by the prefrontal cortex. This suggests an initial subconscious response to potentially threatening stimuli, which can be modulated by top-down control in non-phobic individuals when consciously perceived.

However, these findings are contentious. Subsequent functional magnetic resonance imaging (fMRI) studies failed to demonstrate an amygdala response to subliminal threat-related images in non-phobic individuals (Hoffmann, Lipka, Mothes-Lasch, Miltner, & Straube, 2012), including masked spider images (Lipka, Miltner, & Straube, 2011). Instead, the latter study could only demonstrate amygdala activation to masked spider images in people with arachnophobia (i.e. fear of spiders). This subliminal amygdala activation was positively correlated with an individual's level of vigilance for spider stimuli (e.g. excessive environmental threat monitoring), leading Lipka et al. (2011) to propose that a lack of stimulus-specific vigilance in non-phobic individuals may explain the absence of differential amygdala response during subliminal processing.

It has been suggested that the amygdala responds to biologically critical stimuli to permit their rapid visual processing (Aldophs, 2008; Sander, Grafman, & Zalla, 2003), which facilitates the necessary physiological / behavioural responses preconsciously and helps determine if a stimulus will reach conscious awareness (Diano, Celeghin, Bagnis, & Tamietto, 2017). LeDoux (1995) proposed that sensory information is able to access the amygdala via two pathways: a slow cortical pathway known as the 'high' road, which involves processing by the primary sensory cortices, and a fast subcortical route known as the 'low' road, which bypasses the primary sensory cortices. Accumulating evidence from human and animal studies

suggests that the latter pathway to the amygdala involves connections through the superior colliculi and pulvinar nuclei (Diano et al., 2017; McFadyen, Mermillod, Mattingley, Halász, & Garrido, 2017). Indeed, studies examining subliminal processing using functional neuroimaging often report activation in these three areas in response to invisible stimuli (Jiang & He, 2006; Morris, Öhman, & Dolan, 1999; Pasley, Mayes, & Schultz, 2004; Troiani & Schultz, 2013).

Few behavioural priming studies have examined the subconscious processing of threatening animal stimuli. Under visible conditions, Haberkamp, Schmidt, and Schmidt (2013) examined the visual processing of spiders, snakes, and neutral stimuli in people with arachnophobia, people with ophidiophobia (i.e. fear of snakes), and people without a phobia. They found faster responses to threatening stimuli during a classification task but only when participants were phobic to the specific animal presented. Given that Carlsson et al.'s (2004) study described earlier demonstrated an initial amygdala response to subliminal spider and snake stimuli regardless of whether participants were phobic to them or not, it is possible that priming effects may be observed for subliminally presented snakes and spiders in both phobic and non-phobic participants.

A study by Almeida et al. (2008) examined the subliminal processing of non-threatening animals. They found priming effects when participants were asked to indicate whether a visible target was a tool or an animal using a visual masking but not a CFS paradigm. This suggests that subconscious processes extracted information from the prime to facilitate the discrimination of a subsequent congruent target at a general, superordinate level (animal vs non-animal) in the visual masking paradigm. Whether or not this can occur at a more specific semantic level (i.e. its basic level; elephant vs non-elephant) was not explored. Furthermore, it is possible that this subliminal priming could have been demonstrated during both visual masking and CFS if threatening animals such as spiders and snakes were presented. Previous CFS studies have found priming effects for aversive but not neutral stimuli (e.g. fearful or angry vs. neutral facial expressions), and that fearful face stimuli break suppression faster than neutral and happy faces – suggesting that certain threat-specific stimulus attributes allow their subconscious processing under CFS (Faivre, Berthet, & Kouider, 2012; Yang, Xu, Du, Shi, & Fang, 2011; Yang, Zald, & Blake, 2007).

In the present study, we used a priming paradigm to determine whether or not sufficient information can be extracted and processed from a masked image of a threatening animal for the purposes of recognising and classifying it into a specific category during a subsequent visible presentation. Namely, we presented images of spiders and snakes. Participants were asked to indicate whether each image was a spider or a snake. Performance was compared to neutral objects in which participants classified images of cars and houses into one of these two categories. Houses and cars were used as control stimuli rather than non-threatening animals to ensure greater neutrality. Although an animal such as a kitten is non-threatening, it may not be neutral to a participant if they dislike cats or perceive the animal as cute. Cute animals have been found to elicit positive emotions and improve performance on focused attention tasks (Nittono, Fukushima, Yano & Moriya, 2012). The awareness of the prime was suppressed using visual masking in one experiment and CFS in a separate experiment. We hypothesised that priming effects would be observed in both the perceptually visible and invisible viewing conditions for the spiders and snakes, but only during perceptually visible conditions for the cars and houses.

Additionally, perceptual and semantic processing was examined by manipulating the level of overlapping physical and semantic information between prime-target image pairs. Image pairs consisted of either the same exemplar (e.g. snake followed by the same snake),

different exemplars (e.g. snake followed by a different snake), or different animals or objects (e.g. snake followed by a spider). We hypothesised that similar behavioural priming results as demonstrated by Chouinard et al. (2008) under visible conditions would be found for each visible and invisible prime-target pair. Namely, we predicted faster reaction times when prime-target pairs corresponded to the sample exemplar compared to different exemplars and different exemplars compared to different animals or objects.

2. Methods

2.1 Overview

Participants completed one testing session in either the visual masking experiment or CFS experiment. Aside from the technique used to suppress the awareness of stimuli, the two experiments were similar in their design. Each testing session began with a handedness questionnaire and a series of vision tests that assessed eye dominance, visual acuity, and binocular function – in a manner similar to those used in previous studies (Laycock, Sherman, Sperandio, & Chouinard, 2017; Peel, Sperandio, Laycock, & Chouinard, 2018). Following these tests, each experiment involved two sections: Part A, which contained threatening animal stimuli (snakes and spiders), and Part B, which contained neutral object stimuli (houses and cars). The order with which participants completed Parts A and B was counterbalanced using a Latin square. These two sections were comprised of four identical components. First, a threshold measurement task determined the Michelson luminance contrast level (Michelson, 1995) required for the stimuli to break suppression and enter conscious awareness. This was done separately for the animal (snakes and spiders in Part A) and non-animal (houses and cars in Part B) images. The luminance contrast level of stimuli in subsequent sections of the experiment were then set below these values. Second, a recognition task was completed to verify if stimuli at the adjusted contrast level were genuinely presented subconsciously to the participant. Third, participants completed the priming task, which examined whether or not target stimuli were processed more efficiently (i.e. decreased reaction time) when preceded by a visible or perceptually invisible prime stimulus. Fourth, the recognition task was repeated to verify if stimulus suppression remained successful throughout the experiment. Overall, each testing session took approximately 1.5 hours to complete. Approval for this study was granted by the La Trobe University Human Ethics Committee in accordance with the Declaration of Helsinki. All participants provided written informed consent prior to participation and received a gift card for their time.

2.2 Participants

Sixteen participants (9 females, $M_{Age} = 25.25$ years, $SD = 8.84$ years) completed the visual masking experiment and sixteen participants (8 females, $M_{Age} = 23.31$ years, $SD = 9.90$ years) completed the CFS experiment. Inclusion criteria required participants to be right handed and have normal or corrected-to-normal vision. Handedness was verified using a modified version of the Edinburgh Handedness Inventory Questionnaire (Oldfield, 1971). All participants received a score of 70% or higher ($M = 88.75\%$, $SD = 9.92\%$). Visual acuity was assessed with the Snellen chart. All participants had at least 20/40 vision in each eye.

We screened for possible binocular dysfunction using a method similar to those used in earlier studies (Laycock et al., 2017; Peel et al., 2018). In short, this involved participants placing their index finger in front of a single target two meters away (e.g. a door handle).

Participants were instructed to focus their gaze on their finger and indicate how many targets they perceived in the background, and then to fixate on the target and indicate how many fingers they perceived. Typical binocular fusion abilities were assumed if the participant reported two in both conditions. This was the case for all participants included in the CFS experiment. Abnormal responses were reported by three participants in the visual masking experiment. Given that binocular fusion is not imperative for effective suppression during visual masking these participants were still included.

Eye-dominance was assessed using the Miles test (Miles, 1930). This involved participants extending their arms in front of their body and viewing a distant target through a triangular aperture created by placing their thumbs and index fingers together. Participants were considered right eye dominant if this target remained in view after closing their left eye, or left eye dominant if the target remained in view after closing their right eye. Right-eye dominance was found in 22 participants, and left-eye dominance in 10 participants.

2.3 Stimuli and Apparatus

The stimuli consisted of 40 grey-scale exemplar images for each category (spider, snake, car, house; see Fig. 1 for examples). These stimuli had a resolution of 150 dpi and were presented on a grey background (luminance: 40.32 cd/m², RGB: 128, 128, 128) extending 5° of visual angle with participants 57 cm from the monitor. Stimuli varied in orientation and overhead profile (e.g. some cars faced to the left and others to the right). The 40 exemplar images in each category were randomly split into two sets: one set was used during the priming experiment (i.e. our litmus test for establishing subconscious processing) and the other during the other sections of the experiment (i.e. the control tests for the priming experiment). Participants were counterbalanced using a Latin square to use either set during priming.

Stimuli were presented using E-Prime 2.0 software (Psychology Software Tools, Sharpsburg, PA, United States) on a 23-inch liquid crystal display (LCD) monitor (1920x1200-pixel resolution, 60-Hz frame rate). Participants placed their heads on a chin rest and viewed the stimuli at a distance of 57cm. During the CFS experiment, participants viewed stimuli through a mirror stereoscope. To aid binocular fusion, the stimuli were presented behind a fixation point inside a pictorial frame subtending 16° by 16° of visual angle. During the visual masking experiment, no mirror stereoscope was used and stimuli were presented behind a fixation point in the centre of the screen. Participant responses were recorded with a 200a Serial Response Box (Psychology Software Tools, Sharpsburg, PA, USA).

2.4 Procedures for the Visual Masking Experiment

2.4.1 Threshold measurement

In each trial, E-prime randomly selected target stimuli for each category from a set of 20 exemplar images and presented these under visual masking conditions (for details regarding visual masking, see section 2.4.2). The target stimulus' luminance contrast level varied in each trial following a descending staircase design, which began at a Michelson contrast of 100% (143.76 cd/m²). Using a 2-alternative forced choice method, participants verbally expressed what type of stimulus they saw after each trial (snake/spider in part A or car/house in part B). To minimise errors, the experimenter entered these responses using a keyboard. When categorised correctly, the contrast level of the subsequent trial was reduced by 5%. When categorised incorrectly, the staircase 'reversed' and the contrast level of the subsequent trial increased by 5%. This procedure continued for a total of 12 reversals and the final threshold

level for the stimulus set (i.e. snakes and spiders in part A; cars and houses in part B) was calculated as the average of the last 8 switches. The luminance contrast level of the stimuli in subsequent sections of the experiment was then set to 5% below this perceptual awareness threshold, to a minimum of 5%. This helped ensure that the stimuli were reliably suppressed during visual masking while maximising their saliency for each participant.

2.4.2 Recognition task

To ensure participants could not consciously perceive stimuli at the adjusted contrast level, stimulus awareness was examined using a 2-alternative forced choice discrimination task. At the beginning of each trial, the participant fixated on a blank screen for 3,000 ms. Stimuli were then presented in either visible or invisible conditions using forward and backward masking (see Fig. 2a). During invisible conditions, this involved the presentation of a stimulus for 48 ms between two noise masks presented for 96 ms. During visible conditions, the timing of the visual masks varied in that they did not immediately precede and follow the stimulus. Participants were instructed to indicate the type of target stimulus presented to them as quickly and accurately as possible by button press (snake/spider in part A or car/house in part B). There were 80 trials in total: 40 visible and 40 invisible. Trial order for each participant was determined randomly by E-prime. A break period was given after 40 trials. Effective suppression was assumed when invisible stimuli were discriminated at chance level accuracy; namely, between 15 and 25 correct for 40 trials based on a binomial distribution. If accuracy was not within these limits of chance, the previous threshold procedure was repeated and verified again using this recognition task. The visual masking experiment was terminated for two participants after effective suppression could not be established by repeating these procedures twice – resulting in a total of 16 participants who completed the experiment. After completing the priming task (see section 2.4.3), this recognition procedure was carried out again to determine whether or not suppression remained successful throughout priming.

2.4.3 Priming

Each trial began with a blank fixation screen for 3,000 ms. Participants were then presented with a target preceded by either a visible or invisible prime due to forward and backward masking (see Fig. 2b). Prime stimuli were presented in a sequence of events identical to those in the recognition task. Participants were instructed to categorise the target as quickly and accurately as possible by button pressing (snake/spider in part A or car/house in part B). The task consisted of three prime-target pair conditions: Same exemplar (e.g. snake followed by the same snake), different exemplar (e.g. snake followed by a different snake), and different class (e.g. snake followed by a spider) prime-target pairs. To ensure participants responded to the target and not the prime, a 100 ms alerting cue (tone: 100 Hz) sounded through a pair of headphones at target onset. Participants were instructed to only respond to images presented with this auditory cue. Overall, the priming task consisted of 240 trials. There were 120 visible and 120 invisible prime trials. Within these sets, there were 40 same exemplar, 40 different exemplar, and 40 different class trials. A break period was given every 80 trials. The order of trials for each participant was determined randomly by E-prime.

2.5 Procedures for the CFS Experiment

Threshold, recognition, priming, and post-recognition tasks were conducted using the same procedures as the visual masking experiment with the exception that masking was carried out using CFS methods (see Fig. 3). This involved a blank fixation for 3,000 ms, followed by a series of four Mondrian images which were presented to the participant's dominant eye in a

cycling sequential order at a frequency of 10-Hz. Meanwhile, the non-dominant eye was presented with the prime stimulus for 200 ms. We then presented a Mondrian to both eyes for 96 ms to reduce possible afterimages, followed by a blank image to both eyes for 96 ms and then the target stimulus in the non-dominant eye. Critically, the time period between prime presentation and target onset was identical to the visual masking experiment to avoid differences in memory processes. The visible condition was identical to the CFS condition except for the presentation of flashing Mondrian's during prime presentation. The CFS experiment was terminated for four participants when effective suppression could not be established after repeating the threshold and recognition tasks twice – resulting in a total of 16 participants who completed the experiment.

2.6 Data analyses

Statistical analyses were carried out using the Statistical Package for the Social Sciences version 23 (IBM Corporation; Armonk, New York, USA) and GraphPad Prism version 7 (GraphPad Software, Inc.; La Jolla, California, USA). All reported p values accounted for multiple comparisons. Statistical significance was evaluated in reference to an alpha level of .05.

For each experiment, the threshold data underwent paired-samples t-test to evaluate differences between the animal and object conditions. Results from the recognition tasks were analysed with one-sample t-tests to determine if accuracy performance differed from chance. The Bonferroni method was used to correct for multiple contrasts (Abdi, 2007).

Results from the priming task were examined using ANOVA with Valence (Threatening vs Neutral), Visibility (Visible vs Invisible), and Priming Condition (Different Class vs Different Exemplar vs Same Exemplar) as within-subject factors. Mean reaction time scores for accurate trials only were entered into the ANOVA, and effect sizes (partial eta-squared; η_p^2) are reported. Post-hoc pairwise comparisons using Tukey's honest significance difference (HSD) method (Tukey, 1949), which corrected for multiple comparisons, were conducted to further examine interactions and effects found significant by the ANOVA. Cohen's d effect sizes were calculated for pair-wise comparisons, where the difference between two means was divided by their pooled standard deviation (Cohen, 1988).

Bayes factors in favour of the null over the alternative hypothesis (BF_{01}) were calculated to verify the presence of null findings. Unlike null-hypothesis statistical testing, Bayes statistics allows one to make inferences about null results by determining the likelihood of one hypothesis (e.g. the null hypothesis) relative to another (e.g. the alternative hypothesis). Following current norms, BF_{01} values of three or more were considered as indicating substantial support for the null hypothesis (i.e., an absence of priming), and values less than 0.33 to provide "substantial" support for the alternative hypothesis (i.e., a presence of priming) (Jarosz and Wiley, 2014; Jeffreys, 1961; Wagenmakers et al., 2018; Wetzels et al., 2011). In other words, a BF_{01} value of 3 or greater signifies that the null hypothesis is supported at least 3 times more than the alternative hypothesis while a BF_{01} value of less than 0.33 signifies that the alternative hypothesis is supported at least 3 times more than the null hypothesis.

3. Results

3.1 Visual masking experiment results

3.1.1 Threshold measurement

Luminance contrast thresholds for threatening animals ($M = 49.07$, $SD = 16.63$) were higher than those for neutral objects ($M = 29.26$, $SD = 11.87$) ($t_{(15)} = 6.12$, $p < .001$).

3.1.2 Recognition task

As displayed in Fig. 4a, accuracy for invisible stimuli did not differ from chance (50%) both before and after the priming task ($t_{(15)} \leq 1.82$, $p \geq .09$). In contrast, accuracy for visible stimuli was consistently higher than chance ($t_{(15)} \geq 24.79$, $p < .001$). This indicates that stimuli were reliably suppressed throughout the experiment in the invisible condition.

3.1.3 Priming task

Fig. 5a displays the mean reaction times for each condition in the priming task. ANOVA revealed a Valence x Visibility x Priming Condition interaction ($F_{(2, 30)} = 9.66$, $p < .001$, $\eta_p^2 = .39$). In the visible conditions, pairwise comparisons demonstrated that reaction times were faster for same exemplars in comparison to different exemplars ($p < .002$, $BF_{01} < .001$) and different animals or objects ($p < .002$, $BF_{01} < .001$), and reaction times for different exemplars were faster than different animals or objects ($p < .002$, $BF_{01} \leq .003$). We also noted slower reaction times between different threatening animals versus different neutral objects in the visible condition ($p < .002$), which explains further the three-way interaction. There were no significant differences in reaction times for the invisible conditions (all $p \geq .52$). Bayesian paired-samples t-tests did not indicate substantial evidence for the null hypothesis for differences in reaction time during invisible conditions (BF_{01} range: 0.64 – 2.65), except for differences between different objects and different exemplar objects ($BF_{01} = 3.17$). **Table 1 provides effect sizes for the different priming comparisons for both the visible and invisible conditions.**

Accuracy was not analysed given ceiling levels of performance ($M = 96.21\%$, $SD = 2.16\%$, range: 86.22% to 99.97%). However, to rule out the presence of a speed-accuracy trade-off effect, accuracy and reaction time scores for each participant were averaged across all conditions and then correlated (Wickelgren, 1977). No significant correlation was found ($r_{(14)} = .14$, $p = .64$), which indicates the absence of a speed-accuracy trade-off effect.

3.2 CFS experiment results

3.2.1 Threshold measurement

Luminance contrast thresholds for threatening animals ($M = 28.83$, $SD = 22.51$) were not significantly different than those for the neutral objects ($M = 20.95$, $SD = 5.27$) ($t_{(15)} = 1.79$, $p = .09$).

3.2.2 Recognition task

As displayed in Fig. 4b, accuracy for invisible stimuli did not differ from chance (50%) both before and after the priming task ($t_{(15)} \leq 1.45$, $p \geq .17$), while accuracy for visible stimuli were consistently higher than chance ($t_{(15)} \geq 7.36$, $p < .001$) – confirming that stimuli in the invisible condition were also reliably suppressed throughout the CFS experiment.

3.2.3 Priming task

Fig. 5b displays the mean reaction times for the priming task. ANOVA revealed a Visibility x Priming Condition interaction ($F_{(2, 30)} = 19.88$, $p < .001$, $\eta_p^2 = .57$). In visible conditions, pairwise comparisons demonstrated faster reaction times for same exemplars in comparison to different exemplars ($p = .04$, $BF_{01} = .02$) and different threatening animals or neutral objects (p

= .002, $BF_{01} < .001$). There were no significant differences in reaction times for the invisible conditions (all $p \geq .99$). In invisible conditions, Bayesian paired-sample t-tests indicated substantial evidence for the null hypothesis for differences in reaction time between same exemplars and different objects or animals ($BF_{01} = 3.18$) and between different exemplars and different objects or animals ($BF_{01} = 3.87$). Substantial evidence for the null hypothesis was not found for differences in reaction time between invisible different exemplars and same exemplars ($BF_{01} = 2.81$). ANOVA did not reveal a main effect of Valence ($p = .64$) nor did it reveal any interactions between this factor and any of the other factors (all $p \geq .08$). **Table 2 provides effect sizes for the different priming comparisons for both the visible and invisible conditions.**

Once more, accuracy was at ceiling levels ($M = 96.45\%$, $SD = 2.34\%$, range: 92.56% – 99.72%) and therefore the different conditions were not compared with ANOVA. However, to rule out the presence of a speed-accuracy trade-off effect, accuracy and reaction time scores for each participant were averaged across all conditions and then correlated (Wickelgren, 1977). Again, no correlation was found ($r_{(14)} = .17$, $p = .53$), indicating the absence of a speed-accuracy trade-off effect.

4. Discussion

We tested whether or not people can differentiate subliminal images of threatening animal stimuli well enough to classify them into their basic level category (snake or spider). We hypothesised that this would be demonstrated by priming effects for congruent prime-target pairs. That is, the brief presentation of a threatening animal prime, either visibly or invisibly, would facilitate the categorisation of a subsequent category-congruent target as evidence by a facilitation in reaction times. This hypothesis was not supported. In both experiments, priming effects were only observed in the visible condition.

The extent to which perceptual and semantic processing can take place subliminally was also examined. The hypothesis that same exemplars would yield greatest priming followed by different exemplars and then different-class pairs was supported in the visible condition in the visual masking experiment and partially supported in the visible condition in the CFS experiment. In the latter, no differences were observed between different exemplars and different-class pairs. We could find no evidence of perceptual and semantic priming in the invisible condition for either experiment.

4.1 Absence of priming effects during the invisible condition

Although previous research has demonstrated subconscious processing of threatening animal stimuli in terms of changes in physiological arousal and amygdala activation in healthy participants (Carlsson et al., 2004; Fang et al., 2016; Tan et al., 2013), this study was unable to demonstrate behavioural evidence for this kind of subconscious processing. This converges with findings from our previous studies that could not behaviourally demonstrate the subconscious processing of basic object features (Peel et al., 2018) or size aftereffects (Laycock et al., 2017). Other behavioural studies have only demonstrated subconscious processing to snakes and spiders in participants with a phobia for these animals (Lipka et al., 2011; Öhman & Soares, 1994). Thus, it is possible that the present results are consistent with these findings and support the notion that the subconscious processing of threatening animals occurs only if an individual is phobic to a particular species and that this particular species is presented. This

is potentially due to a sustained vigilance for the phobic species, such as heightened alertness and environmental threat monitoring, which lowers the amygdala's response threshold and increases its sensitivity to these specific stimuli (Lipka et al., 2011).

Another plausible explanation for our results is that subconscious processing can only extract coarse information about a visually presented stimulus. Consequently, the classification task in this study (snake vs spider) might have been too specific to measure subconscious priming effects. In support of this idea, a priming study by Koivisto and Rientamo (2016) found that animal prime images suppressed by CFS facilitated the classification of congruent-category targets at a superordinate level (animal vs. non-animal) but had no effect on classification at a basic level (dog vs. non-dog). Thus, the absence of priming effects during the invisible condition in this study may reflect the inability to subconsciously discriminate within the same valence / threat level or between specific animal species, which requires more fine-grained detail than between the broader categories of animals versus non-animals. This could lend support to the “course-to-fine” model of visual processing positing that a coarse representation of sensory input is constructed through a subconscious feedforward movement of information from lower to higher visual areas in the visual hierarchy (Campana & Tallon-Baudry, 2013). This coarse representation is then supplied with finer details during conscious re-entrant processing, a mechanism which is disrupted during stimulus suppression by visual masking or CFS (Campana & Tallon-Baudry, 2013).

4.2 Presence of priming effects during the visible condition

As predicted, priming effects were demonstrated for both threatening animals and neutral objects when participants were consciously aware of the prime stimulus. This finding converges with previous priming studies wherein the experience of a visible prime facilitates the response to a subsequent related target, reflecting the activation of a particular representation by the prime in memory processes (Wiggs & Martin, 1998). Consistent with Chouinard et al. (2008), priming effects observed in the visual masking experiment were present but at a reduced magnitude when the prime was of the same category as the target but its specific perceptual features were changed. This indicates the presence of both perceptual and semantic processing mechanisms. When same exemplars were presented, priming effects were greatest because both perceptual and semantic features were repeated. When different exemplars were presented, some semantic information was extracted from the prime to facilitate the classification of a related but physically different target stimulus. In other words, the reduction in priming for the different exemplars indicates that these effects are driven by the activation of a unifying pre-existing representation of the stimuli rather by the processing of specific features (Schacter, Dobbins, & Schnyer, 2004).

Previous research has found no differences in the magnitude of priming effects between visible threatening animals and neutral control stimuli in non-phobic participants (Haberkamp et al., 2013). Unexpectedly, a difference was found in this study where responses to threatening animals were significantly slower than neutral objects in the visible different-class condition in the visual masking experiment. It is possible that this result is due to a tendency to dwell on fear-relevant stimuli as proposed by the delayed disengagement hypothesis (Belopolsky, Devue, & Theeuwes, 2011). However, this finding was not replicated in the CFS experiment nor across the different Priming conditions.

4.3 Methodological considerations

To ensure that stimuli were reliably suppressed during visual masking and CFS, luminance contrast levels were measured for each individual using a staircase procedure. The individual differences in contrast sensitivity found in previous studies and the present one demonstrate the importance of using this individualised approach (Zadbood, Lee, & Blake, 2011). Furthermore, the significant difference between threshold levels for animal and object stimuli in the visual masking experiment justifies the use of different threshold levels for the two types of stimuli. This staircase procedure involved a two-alternative forced choice task (Pelli & Bex, 2013). For these reasons, we can be confident that the stimuli were presented subliminally during the invisible condition. This is an important consideration given that previous work claiming to demonstrate subliminal semantic processing (Dehaene and Naccache, 2001) has been criticised for not fully presenting their primes outside of conscious awareness (Kouider & Dupoux, 2004).

We can also rule out the possibility that the priming effects we report reflect mechanisms related to episodic memory. There are two issues to consider. The first is whether or not a prime and a target separated by SOAs of 240 ms in the visual masking experiment and 392 ms in the CFS experiment are sufficiently long enough to form episodic memories. The term episodic memory was first coined by Endel Tulving (1972) in which he made a distinction between conceptual (semantic) memories and remembering events about the past (episodic) – the former being implicit while the latter being explicit. According to a number of influential models of memory (e.g. Baddeley, 2000), 392 ms or less is far too short of a time period to consolidate a memory about an event. The second is whether or not recycling stimuli across trials (e.g. spider X is presented in trial 1 and later in trial 15) might create episodic memories and explain the priming effects we report. The answer is yes to the former but no to the latter. It is important to keep in mind that our data was analysed by comparing different conditions that are conceivably matched in terms of episodic retrieval given that the choice of stimuli presented on each trial was determined randomly. If conditions A, B, and C match in terms of episodic retrieval, it then follows that any differences between them cannot reflect episodic priming. In contrast, we could infer semantic priming by examining differences in reaction times between different exemplars and the different class objects. This is because participants had a life-time experience gathering knowledge about spiders, snakes, cars, and houses prior to the experiment. The presentation of two different exemplars invokes less competing semantic memories than the presentation of two animals or objects that are completely different. Likewise, perceptual priming could be inferred by examining differences in reaction times between the same and different exemplar conditions. This is because the presentation of two identical images requires less visual analyses than the presentation of two images that differ in their physical features.

Another point to consider is whether or not the stimulus-onset asynchronies (SOA) used in this study were suboptimal for detecting priming. Clearly this was not the case in the visible condition. Priming effects with high levels of significance and large effect sizes were observed – underscoring the validity and sensitivity of our procedures under normal conditions. However, SOA length could be a greater concern in the invisible condition whereby the signal of the prime is conceivably weaker and may dissipate faster. Indeed, shorter SOAs are known to yield stronger priming effects in visual masking experiments. Greenwald et al. (1996) recommend using an SOA shorter than 100 ms for visual masking (not CFS) studies based on experiments they performed on words. The reason we did not choose a shorter SOA is that we wanted to introduce a visible condition with the same SOA that differed when the mask was presented between the prime and target. Although our SOA is longer than what is

recommended by Greenwald et al. (1996), it should be noted that what applies to words may not necessarily apply to pictures. Dell'Acqua & Grainger (1999) demonstrated priming with pictures under masking conditions with an even longer SOA (340 ms) than the one we used in our visual masking experiment. Although our SOA for the visual masking experiment is arguably suboptimal, this may not necessarily be the case for the CFS experiment. Longer SOAs are more typical in CFS experiments with some studies demonstrating facilitation effects of the prime on a target with SOAs of up to 3,000 ms (e.g. Bahrami et al., 2010; Zabelina et al., 2013). It is important to consider that the suppression mechanisms of CFS differ from those for visual masking (Almeida, Mahon, Nakayama, & Caramazza, 2008; Almeida, Pajtas, Mahon, Nakayama, & Caramazza, 2013; Fogelson, Kohler, Miller, Granger, & Tse, 2014) and hence optimal timing parameters for one may not necessarily apply to the other. Nonetheless, the visual masking experiment could have been strengthened had a shorter SOA been chosen. Further investigation is required to confirm these interpretations.

Another important consideration is that we did not measure physiological changes such as galvanic skin response, or anxiety / phobia levels towards snakes and spiders. Stimuli were not matched in terms of their familiar size (cars / houses were significantly smaller than their real-world size) or animacy (threatening stimuli were always animals and neutral always non-animals). This may have had unintended influences on results due to an 'animacy effect', where animate objects are remembered better than inanimate objects (Bonin, Gelin, Laroche, Méot, & Bugajska, 2015). Additionally, participants did not perform a "coarse" classification task (e.g. animal vs non-animal or threatening vs neutral). Consequently, the results alone cannot ascertain whether there was a complete absence of subconscious processing or if threatening animal stimuli were subconsciously processed but not at a detailed enough level to make more fine-grained discriminations between specific semantic level categories. This would be a worthwhile exploration for future research. However, based on the present findings, we conclude that the visual processing of threatening animals and neutral objects is facilitated by conscious awareness.

4.4 Concluding remarks

This study investigated the effects of conscious awareness on the processing of threatening animal and neutral object stimuli. In particular, it tested whether or not the subconscious processing of such stimuli could be demonstrated with priming effects during a categorisation task in which participants categorised stimuli at their specific semantic level. Priming effects were only demonstrated in visible conditions in both visual masking and CFS experiments. Thus, no evidence was found to suggest that the visual processing of such stimuli occurs independently of conscious awareness. Future research is required to assess if a coarser representation of a threatening stimulus is able to be subconsciously processed (e.g. its superordinate or valence category). Understanding the possibilities and boundaries of subconscious stimulus processing is not only fundamental to our understanding of the visual system, it also sheds light on the functional role of consciousness. In this study, the findings converge to suggest that subconscious visual processing does not facilitate the perceptual discrimination of threatening animal and neutral object stimuli.

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Declarations of interest: None

Figure legends

Figure 1. Examples of the stimuli used in each experiment. Top row displays threatening animals (spider, snake). Bottom row displays neutral objects (car, house).

Figure 2. Visual masking procedures. Presentation and temporal sequence of events for the recognition task (a) consisting of invisible (left) and visible (right) conditions, and the priming task (b) consisting of invisible (left) and visible (right) conditions.

Figure 3. CFS masking procedures. Presentation and temporal sequence of events for the recognition task (a) consisting of invisible (left) and visible (right) conditions, and the priming task (b) consisting of invisible (left) and visible (right) conditions.

Figure 4. Results from the recognition tasks. Mean \pm SEM accuracy (as a percentage) of discriminating a target stimulus both before (blue/striped bars) and after (green bars) the priming experiment during the visual masking experiment (a) and CFS experiment (b). Asterisks (*) denote significant effects at $p < .05$ after corrections were made for multiple comparisons.

Figure 5. Results from the priming tasks. Mean \pm SEM reaction times (in milliseconds) for the priming task in the visual masking (a) and CFS experiment (b). Asterisks (*) denote significant effects at $p < .05$ and double asterisks (**) denote significant effects at $p < .01$ after corrections were made for multiple comparisons.

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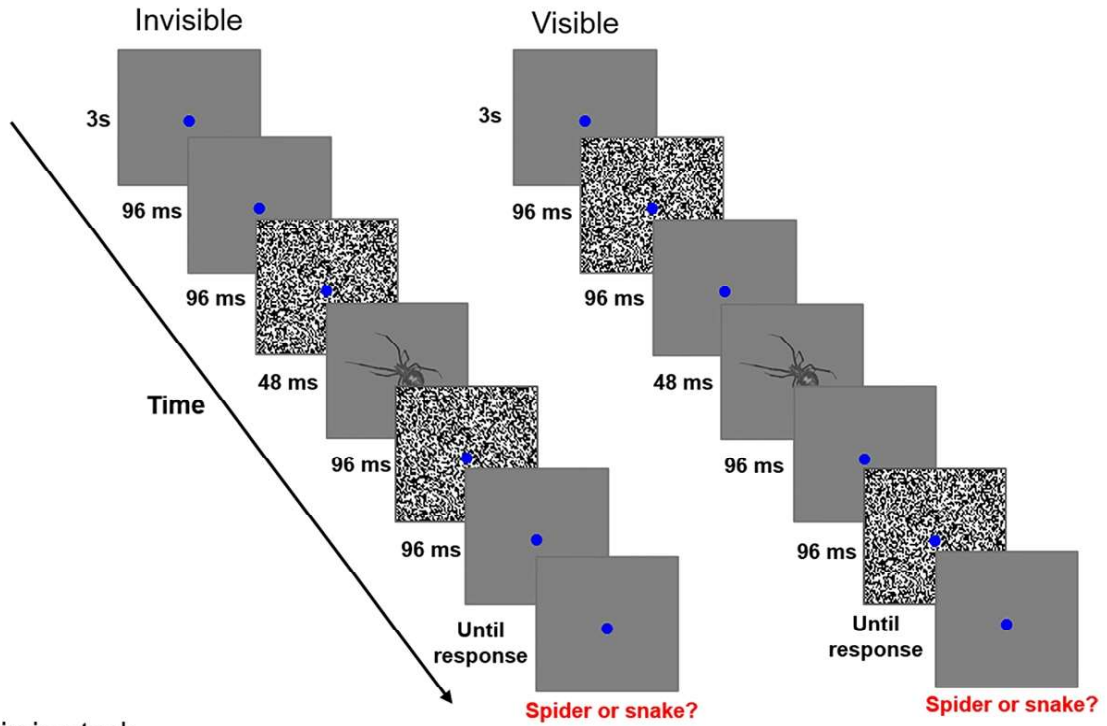
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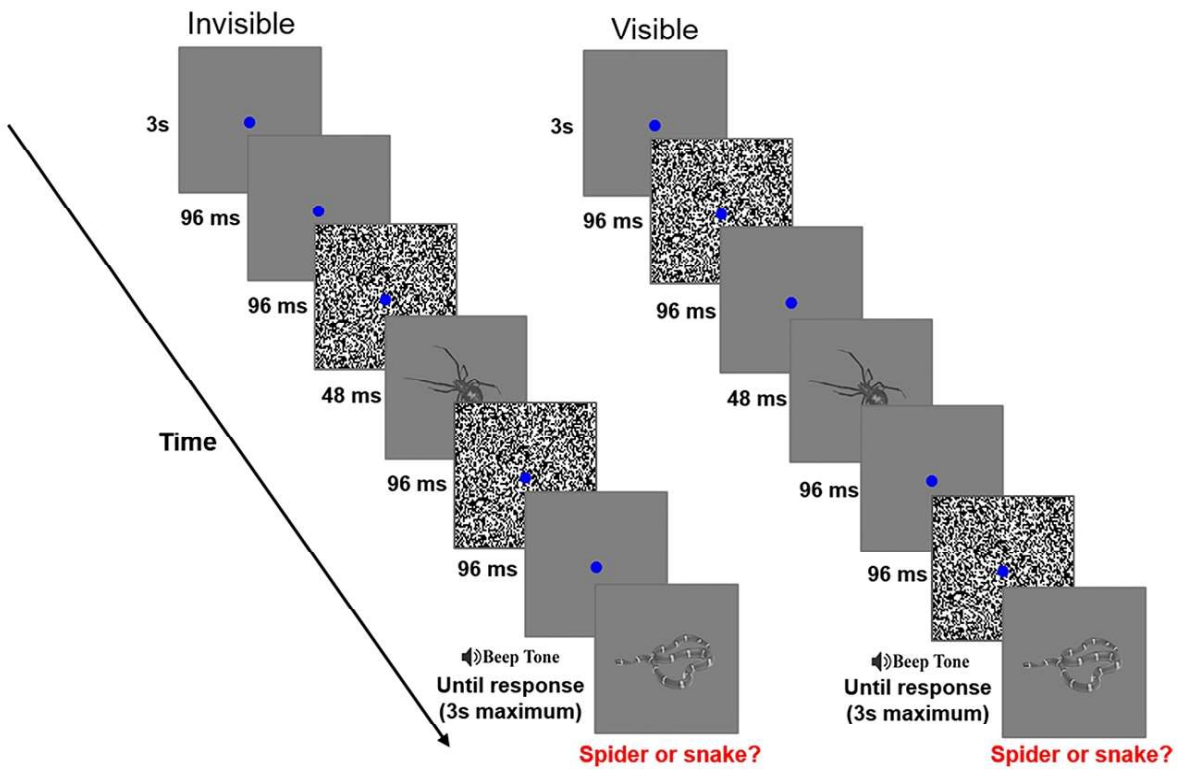
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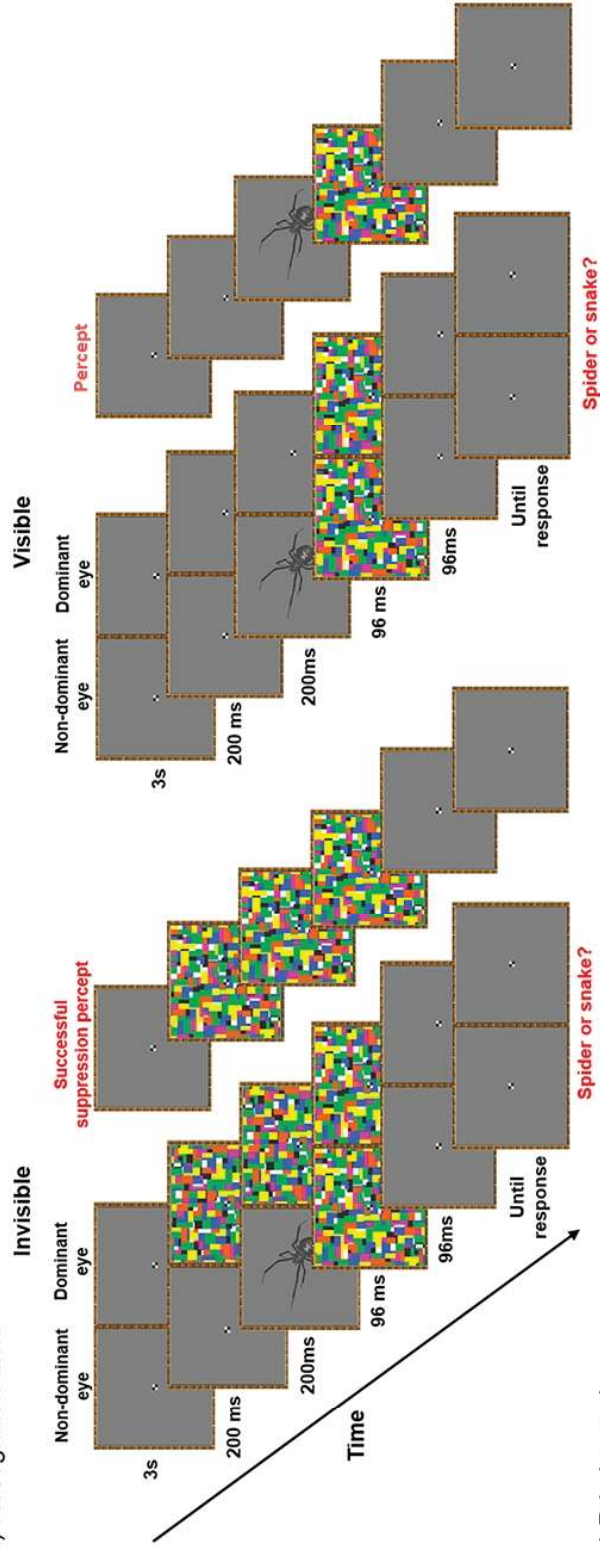
a) Recognition task



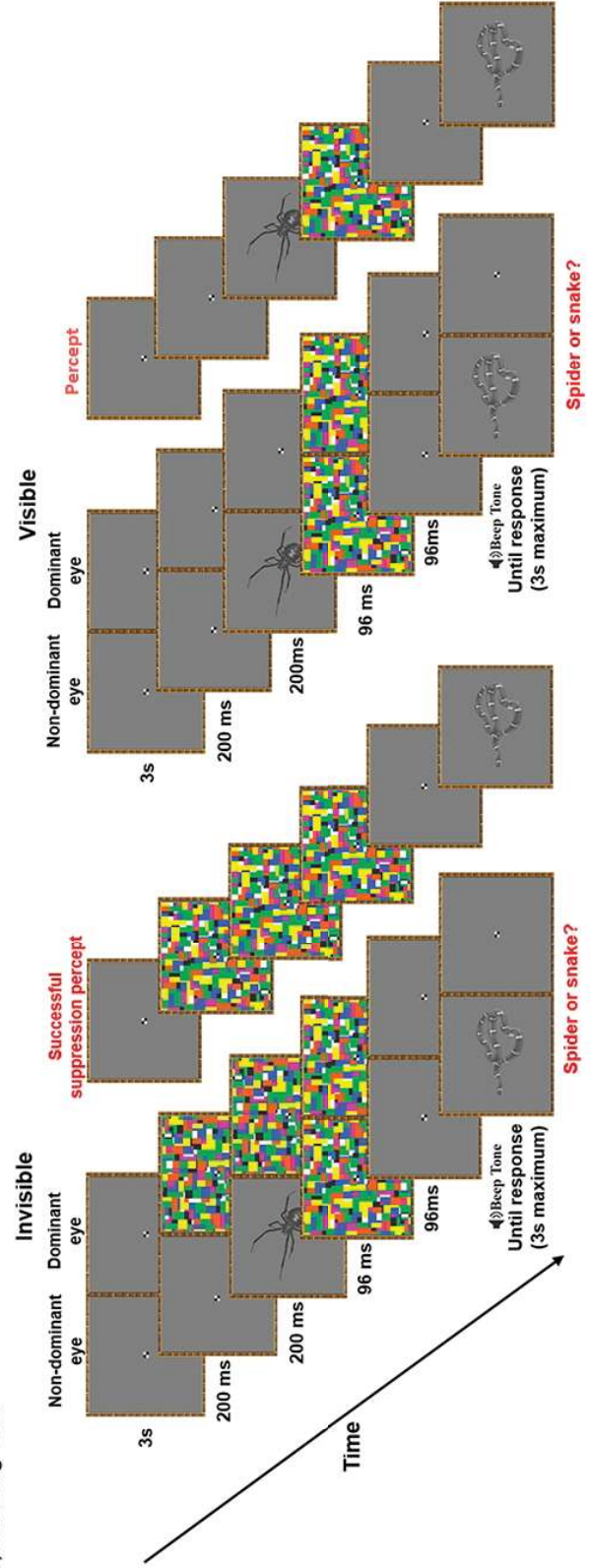
b) Priming task



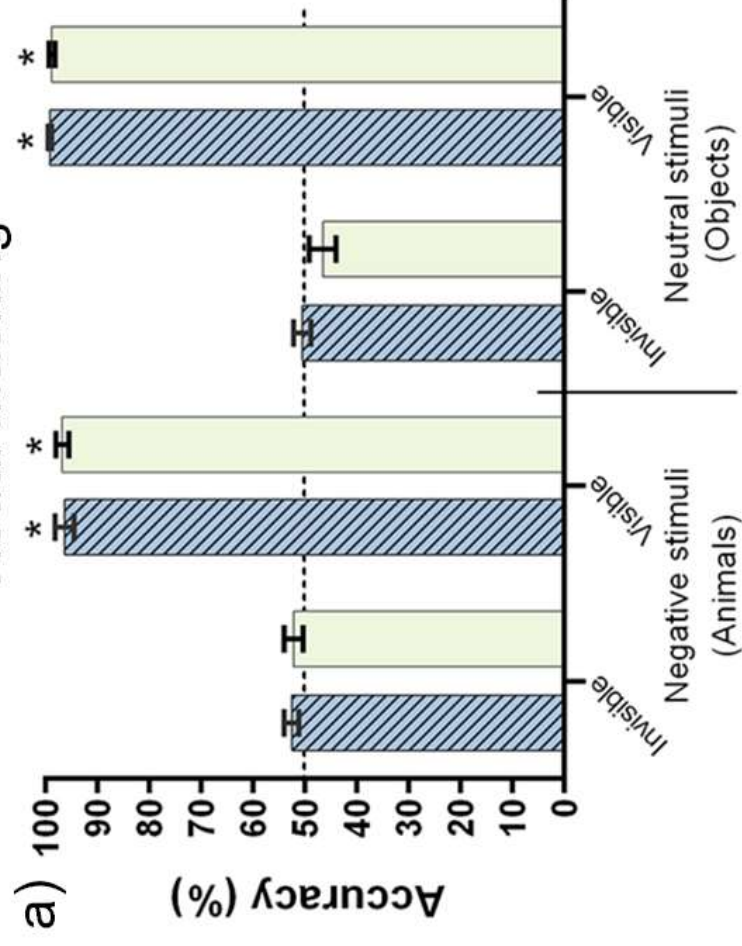
a) Recognition task



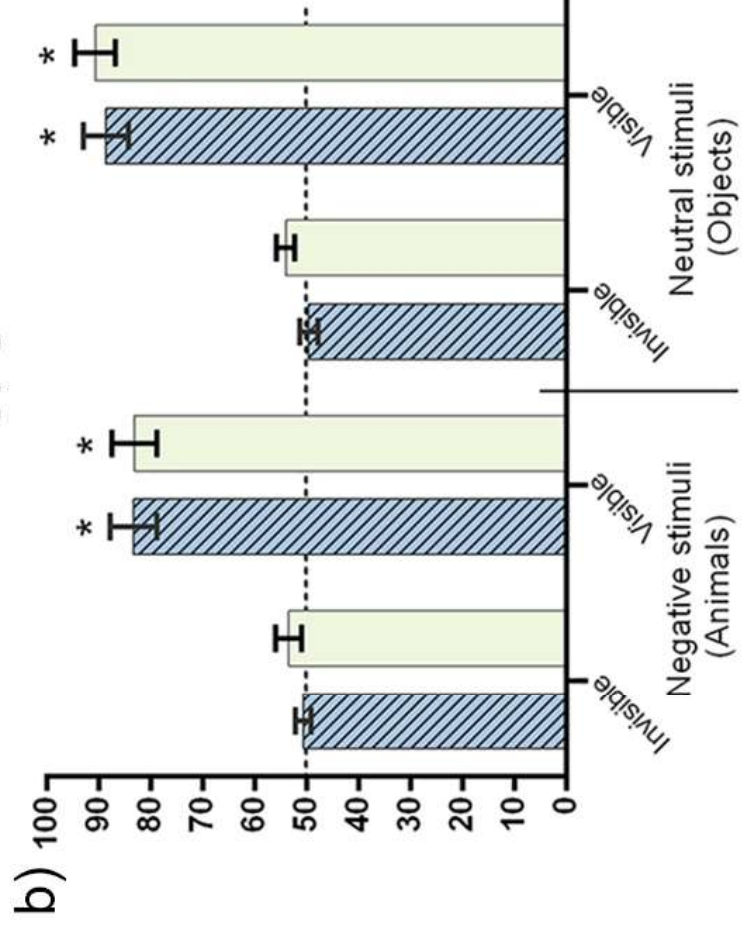
b) Priming task



Visual masking

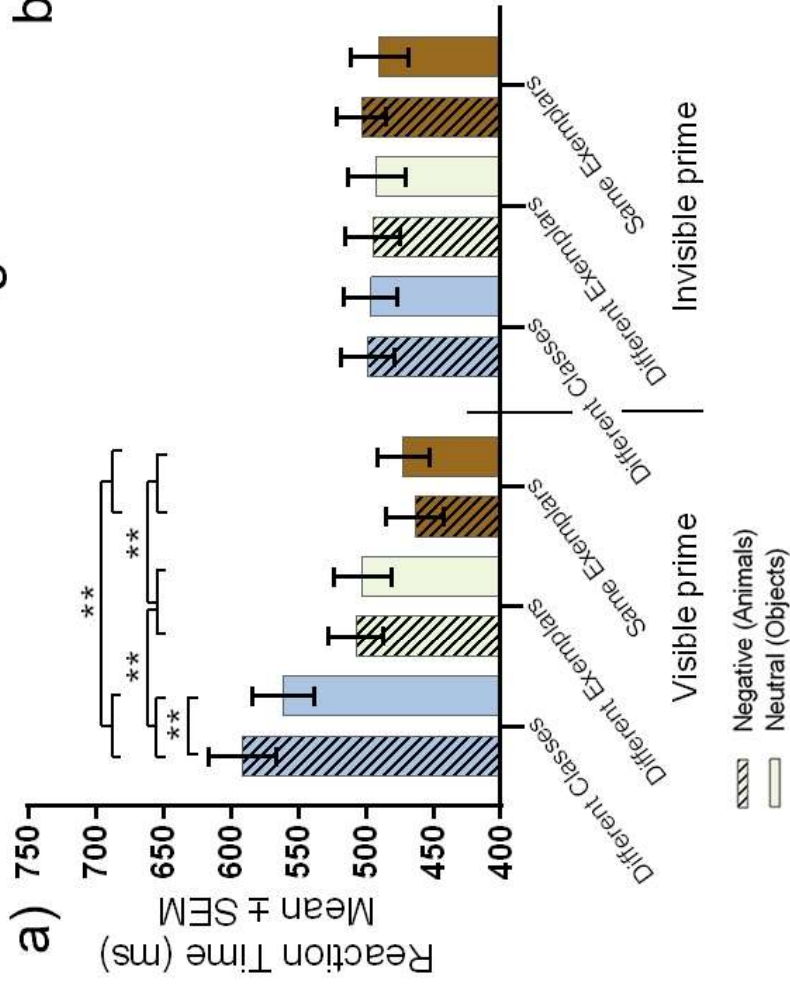


CFS



Pre-Priming Experiment
Post-Priming Experiment

Visual masking



CFS

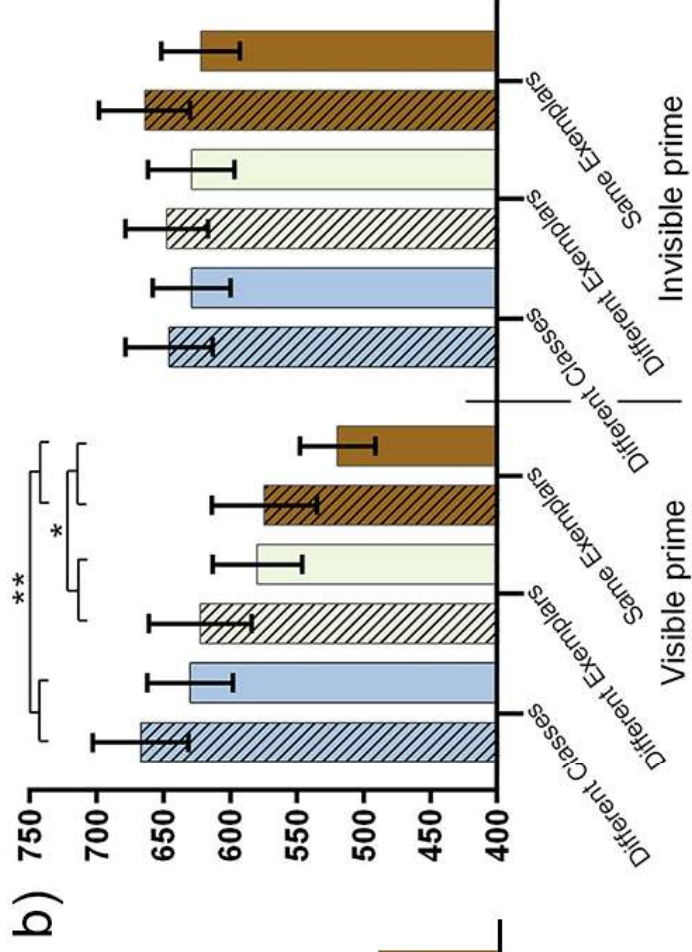


Table 1: Effect sizes for priming comparisons in the visual masking experiment.

Comparison	Visible Prime Cohen's <i>d</i>	Invisible Prime Cohen's <i>d</i>
Different Classes (Negative Animals)	1.41	0.43
Different Classes (Negative Animals)	3.03	-0.32
Different Exemplars (Negative Animals)	1.72	-0.54
Different Classes (Neutral Objects)	1.35	-0.17
Different Classes (Neutral Objects)	1.76	0.27
Different Exemplars (Neutral Objects)	1.16	0.24

Positive Cohen's *d* denotes priming effects in the expected direction while negative Cohen's *d* denotes priming effects in the opposite direction.

Table 2: Effect sizes for priming comparisons in the CFS experiment.

Comparison		Visible Prime Cohen's <i>d</i>	Invisible Prime Cohen's <i>d</i>
Different Classes (Negative Animals)	vs.	0.85	-0.05
Different Classes (Negative Animals)	vs.	1.04	-0.35
Different Exemplars (Negative Animals)	vs.	0.85	-0.37
Different Classes (Neutral Objects)	vs.	0.84	0.00
Different Classes (Neutral Objects)	vs.	1.93	0.20
Different Exemplars (Neutral Objects)	vs.	1.17	0.19

Positive Cohen's *d* denotes priming effects in the expected direction while negative Cohen's *d* denotes priming effects in the opposite direction.