Priming in a shape task but not in a category task under continuous flash suppression

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Continuous flash suppression (CFS) is an interocular suppression technique that uses high-contrast masks flashed to one eye to prevent conscious perception of images shown to the other eye. It has become widely used due to its strength and prolonged duration of suppression and its nearly deterministic control of suppression onset and offset. Recently, it has been proposed that action-relevant visual processing ascribed to the dorsal stream remains functional, while processing in the ventral stream is completely suppressed, when stimuli are invisible under CFS. Here we tested the hypothesis that the potentially dorsal-stream-based analysis of prime-stimulus elongation during CFS affects the categorization of manipulable target objects. In two behavioral experiments, we found evidence for priming in a shape task, but none for priming in a category task, when prime stimuli were rendered invisible using CFS. Our results thus support the notion that the representation of CF-suppressed stimuli is more limited than previously thought.

Introduction

For decades, visual processing at the verge of conscious perception has been an intense area of research in the scientific study of consciousness (Dehaene & Changeux, 2011; Kouider & Dehaene, 2007). Psychophysical and neurophysiological research in healthy observers has used various noninvasive experimental "blinding" methods to suppress visual input from consciousness and examine which features of images and objects are processed on an unconscious level but can still induce effects on subsequent behavior (Bachmann, Breitmeyer, & Ogmen, 2007; Kim & Blake, 2005). A recently introduced method called continuous flash suppression (CFS) has become widely used[1] due to its strength of suppression, as well as its prolonged suppression duration of up to several seconds and almost perfect temporal control of suppression onset and offset (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). CFS is an interocular suppression technique that uses high-contrast dynamic masks on one eye to suppress perception of images presented to the other eye. It has been argued that CFS will act as a "game changer" in consciousness research due to its seemingly unlimited potential to present various kinds of visual stimuli unconsciously for extended periods of time (Sklar et al., 2012; but see Hesselmann & Moors, 2015). However, the level of visual processing which remains intact under CFS is a controversial topic (Gayet, Van

der Stigchel, & Paffen, 2014; Hesselmann, 2013; Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014; Yang, Brascamp, Kang, & Blake, 2014).

Recently, Breitmeyer (2014b, 2015) reviewed most of the standard suppression methods and placed them in a functional hierarchy of unconscious visual processing. In his review article (2015), Breitmeyer locates CFS in the midrange of the functional hierarchy, arguing that it leaves semantic processing intact, though previously it was believed to disrupt even early visual processing and thus ranked much lower on the scale in Breitmeyer's earlier book chapter (2014b). Beyond the question of CFS's absolute and relative placement within the functional hierarchy, another hypothesis proposes that action-relevant visual processing ascribed to the dorsal stream remains functional, while processing in the ventral stream is completely suppressed, when stimuli are invisible under CFS (Lin & He, 2009; Ludwig & Hesselmann, 2015). The finding of largely preserved dorsal activity in a functional magnetic resonance imaging (fMRI) study (Fang & He, 2005) inspired a series of behavioral priming experiments showing that brief presentations of manufactured manipulable objects (tools) that were rendered invisible by CFS influenced subsequent responses to fully visible tool images in a two-alternative forced-choice (2AFC; tool vs. animal) category-discrimination task (Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2008). Specifically, elongated tool primes (e.g., hammer) elicited faster categorization responses for elongated tool targets compared with nonelongated animal primes (e.g., cow). Priming effects for animal targets were not significant.

The conclusion of a CFS priming effect specific to the action-relevant tool category was challenged by the result that elongated stimuli of different categories (images of vegetables and geometric lines) had a similar facilitatory influence on response times (Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012). This finding suggests that such seemingly high-level category effects may be explained by basic visual properties such as elongation (Hebart & Hesselmann, 2012). In their most recent set of experiments measuring priming as well as reaching trajectories, Almeida et al. (2014) argued against a shape-priming account and instead proposed that "this dorsal-stream-based analysis of elongation along a principal axis is the basis for how the dorsal visual object processing stream can affect categorization of manipulable objects" (p. 319). Importantly, however, none of the experiments included the presentation of nonelongated tool targets, thus allowing for the possibility that participants based their responses exclusively on stimulus elongation.

In our first experiment, we therefore aimed to rule out this possibility and verify whether stimulus elongation can indeed be extracted under CFS and thereby facilitate the categorization of manipulable objects (Almeida et al., 2014). We presented both elongated and non-elongated tools and animals, and tested the prediction that elongated prime stimuli, irrespective of prime category, affect the speeded categorization of tool targets, irrespective of target elongation.

Experiment 1

Methods and materials

Participants

We determined sample size based on a recent study by Almeida et al. (2014). In that study, the effect of interest was the role of elongation in visual recognition of manipulable objects. Elongated tool primes (e.g., hammer), as well as elongated animal primes (e.g., fish), elicited faster categorization responses for elongated tool targets when compared with nonelongated ("stubby") animal primes (e.g., cow). The mean effects were 12 ± 4 and 8 ± 3 ms, respectively, and both were significant when tested against zero, $t(26) = 3.08$, $p = 0.005$, and $t(26) = 2.43$, $p = 0.022$ (Almeida et al., 2014, experiment 1a). By contrast, nonelongated tool primes did not result in significantly faster categorization responses for elongated tool targets when compared with nonelongated animal primes (4 ms), $t(26) < 1$. In previous studies, these three response-time (RT) differences defined the pattern of the "category-by-shape" priming account.

Using G*Power 3.1.9 (Faul, Erdfelder, Lang, & Buchner, 2007), we first calculated the associated effect sizes based on the mean and standard deviation of difference ($d_z = 0.58$ and 0.51, respectively). We then determined that for the average effect size of $d_z = 0.55$ and type I error probability of $\alpha = 0.05$, a sample size of $N = 22$ was required to achieve a power of 0.80 (*t* test for matched pairs, one-sided). Twenty-nine observers participated in Experiment 1, which was conducted at the Department of Psychiatry and Psychotherapy, Charité–Universitätsmedizin Berlin, Germany, with ethics approval from the German Association of Psychology (Deutsche Gesellschaft für Psychologie). Participants were recruited from a student pool via email and paid 8 euros/hr for their participation. Four participants were excluded from further analyses because they showed significant above-chance forced-choice discrimination performance for invisible stimuli in the first control experiment. Two additional participants were excluded because they reported too few prime stimuli as invisible in the main experiment (for details on the exclusion criteria, see Exclusion of participants, later). All 23 remaining participants (14 women, nine men; mean age: 23 years; range: 18–34)

had normal or corrected-to-normal vision, were unaware of the purpose of the study, and provided informed written consent.

Apparatus and setup

Participants were seated in a dark environment, the only light coming from the experimental monitor and a second monitor, and viewed the dichoptic images on a 17-in. CRT monitor (SAMTRON 98PDF; effective screen diagonal: 43.6 cm; refresh rate: 60 Hz) via a mirror stereoscope. To stabilize head position, the participants placed their heads on a chin rest. The viewing distance from the eyes to the screen (including distances within the mirror system) was 66 cm. All stimuli were generated using an IBM-compatible PC with an ATI FireGL V7100 graphics card and PsychToolbox 3 (Brainard, 1997; Pelli, 1997) running on MATLAB R2007b (MathWorks Inc., Natick, MA).

Stimuli

Four categories of visual stimuli were used in this experiment: images of manufactured manipulable objects (tools) and images of animals, either elongated or nonelongated. Images from the tool category were the same as in a previous study from our group (Ludwig, Kathmann, Sterzer, & Hesselmann, 2015). There were 10 exemplars in each category (see Supplementary Figure S1 for all exemplars). All 40 grayscale images (400 × 400 pixels) were slightly smoothed (low-pass filtered) using a circular Gaussian filter with a standard deviation of 30 cycles/image in the frequency domain. The low-level image properties (luminance histograms and rotational average of the Fourier spectra) were matched across all exemplars (of all categories) with the SHINE toolbox (Willenbockel et al., 2010). In contrast to previous studies (Almeida et al., 2008; Almeida et al., 2010; Almeida et al., 2014; Sakuraba et al., 2012), we did not add random noise to the preprocessed images. As shown in Supplementary Figure S2A, all elongated stimuli (tools and animals) had a width/length ratio ≤0.4, while all nonelongated stimuli had a width/length ratio >0.4 (width orthogonal to the longest extension). Note that similar ratio distributions can be found for the tool stimuli used in the studies by Sakuraba et al. (2012) and Almeida et al. (2014). With respect to stimulus orientation, we aimed for an approximate matching of orientations between the two elongated-stimulus categories; Supplementary Figure S2B shows the orientations of all stimuli used in Experiment 1.

Interocular masking

We used CFS to render the prime stimuli invisible (Tsuchiya et al., 2006; Tsuchiya & Koch, 2005). CFS uses high-contrast dynamic images (masks) flashed to one eye to suppress images presented to the other eye from awareness. The mask images consisted of colored rectangles and circles whose sizes ranged from 4% to 18% of the size of the CFS area, which measured 8.19° × 8.19°. The rectangles and circles were positioned at random locations on the mask image. Twenty-five of these images were created and flashed in random order at 10 Hz to the dominant eye (Figure 1A). A white square frame was presented around the stimuli to promote stable binocular fusion during dichoptic presentation. Throughout each trial, a central red fixation cross was presented (0.26°); during the presentation of the prime stimulus, the fixation cross was shown only to the dominant eye. The dominant eye was determined using a hole-in-card test (Miles, 1930).

Procedure

In total, the experiment lasted approximately 90 min. Written instructions familiarized participants with all stimuli used in the experiment. Prior to the main experiment, a training session acquainted participants with the procedure and task. In the main experiment, visible targets were preceded by either a suppressed prime stimulus or a blank. On each prime-present trial, the prime stimulus was presented together with the CFS masks for 200 ms (Figure 1A). In prime-absent trials, a blank stimulus and the CFS masks were presented. These trials allowed us to compare visibility ratings in prime-present and prime-absent trials under full suppression; RTs in prime-absent trials were not analyzed. After the prime (or blank) stimulus, the visible target stimulus was presented to both eyes for 2000 ms.

All combinations of prime and target category (tools: elongated and nonelongated; animals: elongated and nonelongated) were presented, yielding 16 prime-present and four prime-absent conditions. Thirty-two trials per condition were presented, resulting in a total of 640 trials. Trial order was randomized. Prime and target exemplars were chosen pseudorandomly on each trial, so that prime and target exemplars were never identical. There were self-paced breaks after blocks of 64 trials. Each block started with an instruction screen illustrating the assignments of the response keys, which were counterbalanced across participants. Participants used the left and right arrow keys to indicate the target category (2AFC: tool versus animal, irrespective of shape), and they were instructed to respond as quickly and as accurately as possible. No feedback was provided. After the speeded response, participants were asked to provide their subjective visibility rating for the prime stimulus according to the perceptual awareness scale (PAS; Ramsoy & Overgaard, 2004). Participants were made familiar with the levels of the PAS during
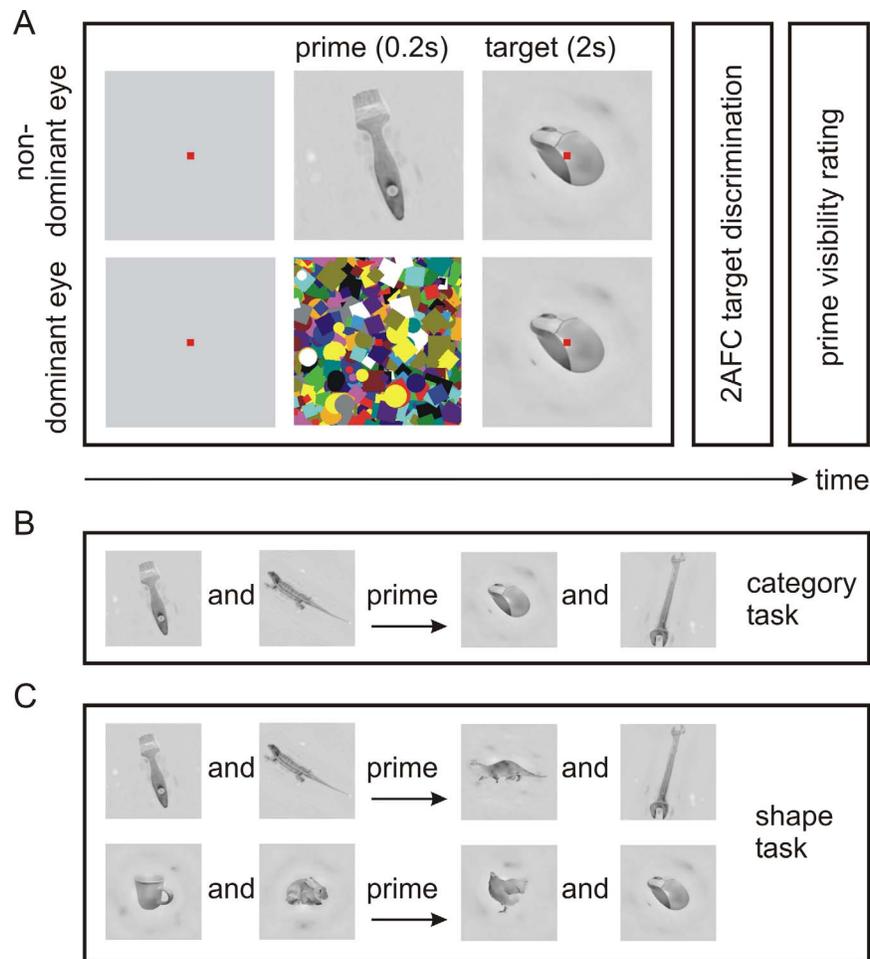
Figure 1. Stimulation and task. (A) The CFS priming paradigm. Using a mirror stereoscope, prime stimuli were presented for 200 ms to participants' nondominant eye (ND), while colored Mondrian masks were flashed at 10 Hz to the dominant eye (D). Targets were presented for 2000 ms to both eyes. In each trial of the main experiment, participants had to report whether the visible target was a manipulable object (tool) or an animal (category task), or whether it was elongated or nonelongated (shape task), and then rate the visibility of the suppressed prime using the PAS. Shown is a trial with an elongated tool (as prime) and an elongated animal (as target). (B) Category task: Illustrated is the prediction that prime elongation (irrespective of category) affects the recognition of tools (irrespective of elongation). (C) Shape task: Illustrated is the prediction that prime shape affects shape discrimination of target stimuli.

training. On each trial, the four levels of the PAS were vertically presented on the screen ("no impression," "weak glimpse," "almost clear," "fully visible"), and participants used the up and down arrow keys to move a cursor and select their rating. The cursor randomly preselected one of the PAS ratings on each trial. By pressing the space bar, participants confirmed their rating and initiated the next trial, which started after a delay of 500–750 ms.

Prime contrast

One of the features of CFS is its large interindividual variability in terms of suppression strength and contrast dependency. In a recent study using a 370-s long CFS display, dominance durations varied 130-fold between participants (Yamashiro et al., 2014). CFS suppression levels have also been shown to change across trials, so that contrasts need to be adjusted in order to maintain stimulus invisibility (Ludwig, Sterzer, Kathmann, Franz, & Hesselmann, 2013). To control for this variability, our approach was to individually adjust contrast levels prior to the main experiment and run objective awareness checks afterwards. We adjusted prime contrasts following a staircase procedure, as follows: After a stimulus presentation that conformed to that of the main experiment, participants had to press a key according to whether the stimulus had been visible or not. Based on this response, the stimulus contrast was decreased or increased following a logarithmic scale in the next trial (one-up-one-down staircase). Each participant completed two staircases of 20 trials. The stimulus contrast in the main experiment was set to the highest stimulus contrast that the

participant always judged as invisible in the pretest. This adjustment of the prime contrast was performed to ensure maximal stimulus strength even under full suppression. The resulting Michelson contrast was 0.27 $\pm$ 0.03 (mean $\pm$ *SEM*).

It is important to note that Almeida et al. (2014) used the same prime contrast for all participants and excluded participants based on awareness checks. In their experiment, about half of the participants (experiment 1a: 48%) were excluded because they were not classified as objectively unaware of or were classified as subjectively aware of the primes. One can argue, however, that the need to exclude 48% of participants indicates a high level of stimulus visibility at the population level prior to exclusion. In statistical terms, restricting the analysis to a small subset of participants may violate the principle of random sampling and capitalize on chance differences between participants (Schmidt, 2015), although it is not clear what percentage defines a problematically small subset. (Note that we excluded 15% of participants in Experiment 1 and 7% in Experiment 2 based on awareness checks.)

First control experiment

The first control experiment served to estimate prime awareness and followed immediately after the main experiment. In this experiment, no targets were presented after the presentation of the suppressed primes. There were no prime-absent trials. Participants were instructed to indicate the category of the primes (tool vs. animal, 2AFC) and provide prime visibility ratings. Participants were instructed to guess the prime category if the primes were invisible. A total of 100 trials were presented. Importantly, the order of experiments ensured that potential training effects on prime processing during the course of the main experiment could be detected in the first control experiment (Ludwig et al., 2013). Furthermore, the same level of suppression (i.e., all primes fully suppressed) was used in both experiments, to avoid an underestimation of prime awareness based on the first control experiment and thus an overestimation of unconscious prime processing during the main experiment (Lin & Murray, 2014).

Second control experiment

In the second control experiment, we sought to test to what degree participants were able to discriminate the primes when they were presented as in the main and first control experiment (i.e., briefly and with low contrast) but without the CFS masks. No targets were presented after the presentation of the primes, and as before, participants were instructed to indicate the

category of the primes and provide prime visibility ratings. A total of 80 trials were presented.

Familiarity and manipulability ratings

After the three experimental sessions, participants rated all 40 stimuli on two dimensions. Following Salmon, McMullen, and Filliter (2010) we used a 5-point Likert scale for familiarity ("rate your familiarity with the object or the degree to which you come into contact with or think about the concept on a day-to-day basis") and manipulability ("rate the manipulability of the object according to how easy it is to grasp and use the object with one hand").

Exclusion of trials

In the main experiment, only data from trials with correct responses were analyzed. We discarded RTs that were 1.5 interquartile ranges above the third quartile or below the first quartile with respect to the individual distribution of all correct RTs (Tukey, 1977). To further minimize the effect of outliers, trials with anticipatory responses (RT < 100 ms) were excluded as well (Whelan, 2008). Following this definition, 7.58% of correct trials were RT outliers and were removed from further analysis. As an alternative approach, we first excluded trials with RTs <150 ms and >3000 ms; in a next step, trials with RTs more than three standard deviations above or below the mean were excluded, based on the individual RT distributions. Following this "mean ± 3 *SD*" definition, 2.13% of correct trials were RT outliers. We reasoned that strong priming effects should be robust to using either of these outlier definitions.

Exclusion of participants

In the first control experiment, 2AFC discrimination performance for stimuli rated as invisible (PAS = 1) was determined for each participant and submitted to binomial tests (chance level: 50%; α: 0.05). Four participants were excluded because they showed significant above-chance performance (65%, 58%, 80%, and 63%; all *p*s < 0.05). Next we sought to exclude participants with too few prime stimuli rated as subjectively invisible in the main experiment, but at the same time we aimed to keep the number of participants as large as possible and hence statistical power as high as possible. To this end, we first selected participants who gave more "weak glimpse" ratings (PAS = 2) than "no impression" ratings (PAS = 1) in the main experiment. This was the case for six participants. Next we tested for each of these participants whether including the "weak glimpse" trials in the analysis of the first control experiment would yield significant
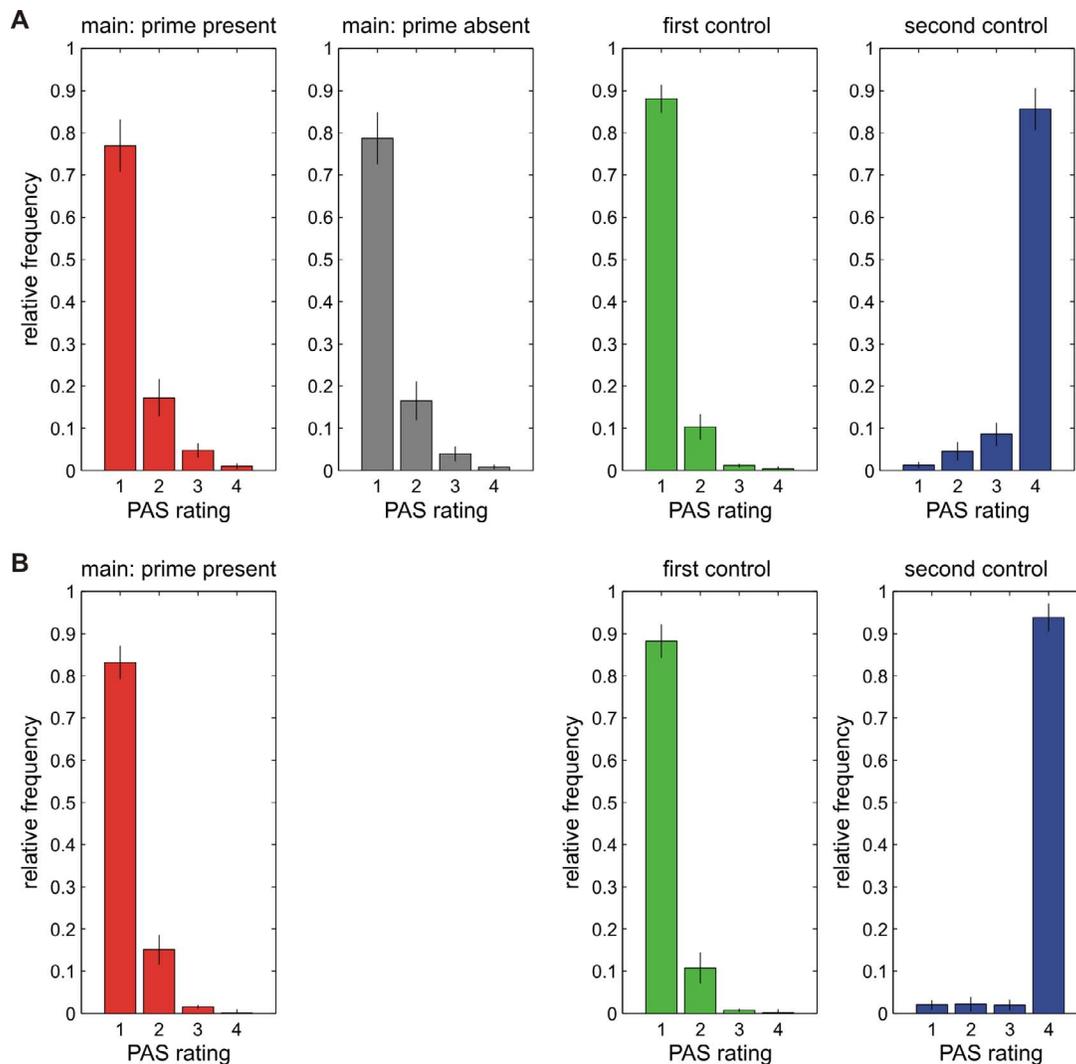
Figure 2. Prime visibility ratings in Experiment 1 (A) and Experiment 2 (B). Plotted are PAS ratings in prime-present (red bars) and prime-absent (gray bars) trials of the main experiment and in the first (green bars) and second (blue bars) control experiment. There were no prime-absent trials in Experiment 2. Plotted is the mean ± standard error of the mean.

above-chance performance; if this was not the case, we included the participant in the main analysis but defined prime invisibility for the participant based on "no impression" and "weak glimpse" PAS ratings (i.e., ratings 1 and 2) as well as chance-level performance in the discrimination task (for a similar approach, see Ludwig et al., 2015). Following this procedure, two of the six selected participants were excluded (59% and 62%; all ps < 0.05). For all remaining 23 participants, Supplementary Figure S3A plots forced-choice discrimination performance in the first control experiment.

Data analysis

To check for the predicted pattern of results already described (also see Figure 1B), RT data were first analyzed using paired t tests, following Almeida et al.

(2014). Next we submitted the data from prime-present trials to a repeated-measures ANOVA with the following factors: Target category (two levels, animals vs. tools), Target elongation (two levels, elongated vs. nonelongated), Shape congruency (two levels, congruent vs. incongruent), and Category congruency (two levels, congruent vs. incongruent). ANOVAs were calculated using IBM SPSS (Version 22.0).[3]

Results

Prime visibility and prime discrimination

Figure 2A summarizes subjective prime visibility ratings in prime-present and prime-absent trials of the main experiment, as well as in the first and second control experiments. In the main experiment, "invisible" ratings (PAS = 1) were most frequent, both in

Target	Prime			
	Elongated tool	Nonelongated tool	Elongated animal	Nonelongated animal
Elongated tool	657 ± 20	652 ± 21	658 ± 19	662 ± 22
Nonelongated tool	665 ± 22	655 ± 19	658 ± 19	659 ± 21
Elongated animal	666 ± 23	654 ± 23	660 ± 22	646 ± 21
Nonelongated animal	656 ± 27	655 ± 23	662 ± 25	658 ± 23

Table 1. RTs (mean $\pm$ *SEM*; ms) in Experiment 1 across participants ($N = 23$).

prime-present (77.00%) and in prime-absent trials (78.74%); intermediate (PAS $= 2$ or 3) and full visibility ratings (PAS $= 4$) were less frequent. Median PAS ratings were highly similar across prime categories (elongated tools: 1.28; nonelongated tools: 1.24; elongated animals: 1.26; nonelongated animals: 1.26). In the first control experiment, which we conducted to estimate objective prime unawareness, primes were predominantly rated as invisible (88.09%). Forced-choice discrimination performance for invisible primes was at chance level (48.87%), $t(22) = -1.41$, $p = 0.172$. In the second control experiment, we sought to test to what degree participants were able to discriminate the primes when they were presented at the individually adjusted contrast levels but without the CFS masks. Primes were predominantly rated as clearly visible (PAS $= 4$; 85.65%), and 2AFC discrimination of visible primes was near ceiling level (97.27%).

RTs in trials with invisible primes

2AFC discrimination of target category (tool vs. animal) was at 97.57%. Table 1 summarizes mean correct RTs in Experiment 1. Since this was the main finding in previous work (Almeida et al., 2014), we first tested whether elongated tool primes as well as elongated animal primes elicited faster categorization responses for elongated tool targets (657 and 658 ms, respectively) when compared with nonelongated animal primes (662 ms). While the observed RT differences were numerically in the predicted direction (5 and 4 ms, i.e., facilitatory), they were not significant (one-sided paired *t* tests), $t(22) = 0.56$, $p = 0.290$, and $t(22) = 0.52$, $p = 0.305$.

If there were a facilitatory effect of prime-stimulus elongation (irrespective of category) on the categorization of tools, then we should expect a significant Target category $\times$ Target elongation $\times$ Shape congruency interaction. The ANOVA showed that this interaction was not significant, $F(1, 22) = 0.67$, $p = 0.421$, $\eta_p^2 = 0.03$. No other main effects or interactions were significant (see Supplementary Table S1 for full ANOVA results). Overall, this pattern of results was robust against using the "mean ± 3 *SD*" outlier definition, which included more trials with long RTs.

Familiarity and manipulability ratings

Average familiarity ratings for the different sets of stimuli (Supplementary Figure S1; one out of 29 participants did not fill out the rating questionnaire) were as follows: elongated tools: 3.81; nonelongated tools: 4.41; elongated animals: 2.90; nonelongated animals: 3.11. An exploratory analysis of manipulability ratings (elongated tools: 4.64; nonelongated tools: 4.68; elongated animals: 1.96; nonelongated animals: 2.06) with factors Category and Shape revealed that tools were rated as significantly more manipulable than animals, $F(1, 27) = 309.54$, $p < 0.001$, $\eta_p^2 = 0.92$; the effect of shape was marginally significant, $F(1, 27) = 4.21$, $p = 0.050$, $\eta_p^2 = 0.14$, while the Category $\times$ Shape interaction was not, $F(1, 27) < 1$. Shape did not influence manipulability ratings of tools, $t(27) = -1.00$, $p = 0.322$.

Discussion

The results from Experiment 1 provide no evidence in support of the hypothesis that elongated prime stimuli that are rendered invisible by CFS facilitate the categorization of manipulable objects due to a "dorsal CFS bias" (Almeida et al., 2014). In contrast to previous CFS studies (Almeida et al., 2008; Almeida et al., 2010; Sakuraba et al., 2012), we observed no priming effects in the tool-versus-animal categorization task. How can this finding be explained? First, this failure to reproduce previous results may be due to random sampling (Francis, 2013)—i.e., even true phenomena sometimes do not yield significant results—and low statistical power in our experiment (Button et al., 2013). Beyond effect size and significance, however, the descriptive analysis of our RT data does not match well with the predicted pattern of RT differences.

Second, there are a number of methodological differences between our experiment and previous studies. Among them is the set of visual stimuli. One could argue that the tool stimuli used in our experiment (Supplementary Figure S1) were less manipulable than the tool stimuli used in previous studies. But participants rated all our tool images, including the non-elongated exemplars, as highly manipulable. Furthermore, the results from our recent fMRI study

(Ludwig et al. 2015), which used the same set of tool stimuli, showed that tool-selective areas in parietal cortex were activated similarly by elongated and nonelongated tool exemplars. We therefore rule out low manipulability of our tool stimulus set as a potential confound. An important basic visual feature of our stimuli is their elongatedness. While the width/length ratios of our stimuli form a bimodal distribution similar to the ratio distributions found in previous priming studies (Supplementary Figure S2), one could argue that the distributions should be not just similar but equal in terms of mean and variance. This, however, was not even the case for two previous studies that both showed significant priming effects (Almeida et al., 2014; Sakuraba et al., 2012). Of note, we deliberately decided to use more exemplars per stimulus category than in previous studies, to minimize potential confounds of stimulus sampling. In studies with few stimulus exemplars it may well be that the observed effects are driven by only a subset of stimuli; this would limit the generalization to future studies involving different samples of stimuli and would remain undetected unless statistical tests were calculated including the stimulus exemplar as a random factor (Judd, Westfall, & Kenny, 2012).

In terms of interocular masking, the types of CFS masks and methods for dichoptic stimulation were different between studies. We used a mirror stereoscope in combination with colored Mondrian masks similar to the masks in the original CFS study (Tsuchiya & Koch, 2005); the studies that reported significant tool priming effects under CFS used anaglyph glasses in combination with monotone random-noise images as masks (Almeida et al., 2008; Almeida et al., 2010; Almeida et al., 2014; Sakuraba et al., 2012). The mirror stereoscope gives no cross talk between the eyes, but the anaglyph glasses produce considerable stereoscopic cross talk (Baker, Kaestner, & Gouws, 2015). While there has been no systematic investigation of the potential influence of the various dichoptic stimulation methods on CFS, the influence of the spatiotemporal mask properties on the strength of CFS suppression has already been investigated. Specifically, Yang and Blake (2012) showed that Mondrian masks composed of only their high-spatial-frequency components yielded much weaker elevation of test-probe detection thresholds (i.e., lower suppression strength) than Mondrian masks that were filtered to contain only their low-spatial-frequency components. Using a similar probe detection technique (Tsuchiya et al., 2006), unpublished data from our lab show that random-noise masks result in lower detection thresholds than Mondrian masks (Supplementary Figure S4). One could therefore argue that the suppression level in our experiment was deeper than in previous CFS priming experiments, which might explain the absence of

priming in our case. By carefully adjusting prime-stimulus contrasts individually for each participant, however, we ensured maximal stimulus strength even under full CFS suppression. On a final note, behavioral and neural effects under CFS appear to be rather robust against smaller changes in the experimental setup; for example, significant cortical responses to invisible stimuli have also been found for Mondrian-like masks (Jiang & He, 2006; Sterzer, Haynes, & Rees, 2008). We conclude that the divergent results are not likely to be due to methodological differences.

Most critically, the conceptual difference between our experiment and previous studies might be the performed task. As pointed out in the Introduction, all tool targets in previous experiments were elongated, while all animal targets were nonelongated. Thus, it is possible that participants performed a shape-discrimination task (elongated vs. nonelongated) rather than the instructed category-discrimination task (tool vs. animal). In our first experiment, participants were unable to use this shape strategy, as targets could be either elongated or nonelongated, irrespective of category (Supplementary Figure S1). In Experiment 2, we sought to investigate this further by testing a new sample of participants with both shape- and category-discrimination tasks in a within-subject design.

Experiment 2

Methods and materials

Methods including apparatus and setup, stimuli, and interocular masking were the same as in Experiment 1, except for the differences described in the following. The main difference between the experiments was the inclusion of a shape-discrimination task in Experiment 2 (see Procedure).

Participants

Thirty-one observers participated in Experiment 2. All 27 participants who were included (16 women, 11 men; mean age: 23 years; range: 18–32; for details on the exclusion criteria, see later) had normal or corrected-to-normal vision, were unaware of the purpose of the study, and provided informed written consent.

Stimuli

Based on the debriefing of participants in Experiment 1, we removed a subset of nonelongated stimuli that were considered less "roundish": exemplars 13, 18, 19, and 20 were removed from the nonelongated-tool

category, and exemplars 39 and 40 were removed from the nonelongated-animal category. We also removed exemplars 8 and 10 from the elongated-tool category; finally, to remove the same number of exemplars from each category, additional exemplars of similar stimulus orientation were excluded (marked in red in Supplementary Figure S1; Supplementary Figure S2B shows the orientations of all stimuli used in Experiment 2).

Procedure

In total, the experiment lasted approximately 90 min. The blank prime condition was removed from the design, yielding a total of $4 \times 4 = 16$ conditions. These were presented in two blocks of 384 trials each; the blocks differed only with respect to the task instruction, which was either a shape-discrimination task (elongated vs. nonelongated) or a category-discrimination task (tool vs. animal). The first 64 trials of each block were discarded as training trials. Each miniblock of 64 trials started with an instruction screen illustrating the assignments of the response keys. The order of blocks and the response-key assignments were counterbalanced across participants.

Prime contrast

Prime contrast was individually adjusted to ensure maximal stimulus strength even under full suppression. The resulting Michelson contrast was 0.65 ± 0.05 (mean $\pm$ *SEM*).

First control experiment

In the first control experiment, two blocks of 60 trials each were presented to estimate prime awareness based on objective performance in both tasks (i.e., category and shape discrimination).

Second control experiment

In the second control experiment, in which primes were shown without the CFS masks, only a single category-discrimination block of 60 trials was presented. We reasoned that above-chance category discrimination of visible primes would imply above-chance shape discrimination of the same primes.

Exclusion of participants

One participant was excluded from further analyses because he pressed the same response button on each "invisible prime" trial in the first control experiment (hence, we assume that he was not guessing as instructed); furthermore, his mean RTs (>1 s) were almost twice as long as the group's mean RTs in the main experiment. Another participant was excluded because he gave very few ratings of PAS = 1 (3.4%) and PAS = 2 (2.5%) ratings in the main experiment, while he rated the suppressed primes as fully invisible (PAS = 1; 99%) during the first control experiment (hence, we assume that he misunderstood the instruction and reported the visibility of the unsuppressed target stimulus during the main experiment; less plausible is the alternative scenario that he might have been "immune" to CFS suppression during the main experiment). In the first control experiment, 2AFC discrimination performance for stimuli rated as invisible (PAS = 1) was determined for each participant and submitted to binomial tests, separately for the shape- and category-discrimination tasks (chance level: 50%; α: 0.025). Two further participants were excluded because they showed significant above-chance performance; one was above chance in the shape-discrimination task (63%), and the other was above chance in the category-discrimination task (68%).

As in Experiment 1, we then selected participants who gave more "weak glimpse" ratings (PAS = 2) than "no impression" ratings (PAS = 1) in the main experiment (two participants) and tested them for above-chance performance in the first control experiment for both visibility ratings. Following this procedure, neither was excluded; their "weak glimpse" trials in the main experiment were included in the analysis. For the resulting 27 participants, Supplementary Figure S3B plots forced-choice discrimination performance in the first control experiment.

Results

Prime visibility and prime discrimination

Figure 2B summarizes subjective prime visibility ratings in Experiment 2. In the main experiment, "invisible" ratings (PAS = 1) were most frequent (83.18%); intermediate (PAS = 2 or 3) and full visibility (PAS = 4) ratings were less frequent. Median PAS ratings were highly similar across prime categories (elongated tools: 1.07; nonelongated tools: 1.11; elongated animals: 1.07; nonelongated animals: 1.11).

In the first control experiment, primes were predominantly rated as invisible (PAS = 1; 88.27%). Forced-choice discrimination performance for invisible primes was at chance level in the shape task (50.96%), $t(26) = 0.73$, $p = 0.475$, and marginally significant in the category task (52.14%), $t(26) = 2.05$, $p = 0.050$. In the second control experiment, primes were predominantly rated as clearly visible (PAS = 4; 93.83%), and 2AFC category discrimination was near ceiling level for visible primes (95.18%).

Target	Prime			
	Elongated tool	Nonelongated tool	Elongated animal	Nonelongated animal
Category task				
Elongated tool	602 ± 17	616 ± 21	607 ± 18	602 ± 15
Nonelongated tool	616 ± 19	626 ± 18	618 ± 20	624 ± 20
Elongated animal	608 ± 19	601 ± 20	611 ± 21	607 ± 21
Nonelongated animal	587 ± 19	591 ± 19	590 ± 18	607 ± 20
Shape task				
Elongated tool	585 ± 15	601 ± 15	593 ± 15	600 ± 16
Nonelongated tool	640 ± 15	649 ± 19	630 ± 16	645 ± 18
Elongated animal	617 ± 13	609 ± 14	607 ± 12	617 ± 13
Nonelongated animal	607 ± 13	610 ± 14	621 ± 14	604 ± 13

Table 2. RTs (mean ± SEM; ms) in Experiment 2 across participants ($N = 27$).

RTs in trials with invisible primes

2AFC discrimination of targets was at 91.83% in the shape task and 96.00% in the category task. The lower discrimination performance in the shape task was due to the fact that some of the participants falsely categorized some nonelongated tool exemplars as elongated. As this false classification was nearly systematic for these participants, it effectively removed trials with these stimuli as targets from their data analysis. Of all correct trials, 6.72% were RT outliers. Based on the alternative "mean ±3 SD" definition, 2.19% were RT outliers.

Table 2 summarizes mean correct RTs in Experiment 2, separately for the category- and shape-discrimination tasks. Overall, RTs were similar for the two tasks (607 vs. 615 ms).

For the category task, we first tested whether elongated tool primes as well as elongated animal primes elicited faster categorization responses for elongated tool targets (602 and 607 ms, respectively) when compared with nonelongated animal primes (602 ms). The observed RT differences were not in the predicted direction and not significant (one-sided paired t tests), $t(26) = -0.01$, $p = 0.498$, and $t(26) = -0.82$, $p = 0.209$.

If there were a facilitatory effect of prime-stimulus elongation on the categorization of manipulable objects (Figure 1B), then we should expect a significant Target category × Target elongation × Shape congruency interaction in the category-discrimination task. The ANOVA showed that this interaction was again not significant, $F(1, 26) = 0.63$, $p = 0.435$, $\eta_p^2 = 0.02$. The main effect of Target category was significant (see Supplementary Table S2 for full ANOVA results) because it took participants longer to categorize tool targets as compared to animal targets (614 vs. 600 ms). Overall, this pattern of results was robust against the "mean ±3 SD" outlier definition, which included more trials with long RTs.

If there were shape priming (i.e., congruent prime shape facilitates target shape discrimination, Figure 1C), then we should expect an influence of Shape congruency in the shape-discrimination task, as either a main or interaction effect. While we found no main effect (see Supplementary Table S2 for full ANOVA results), interactions involving Shape congruency were significant—namely Category congruency × Shape congruency, $F(1, 26) = 5.62$, $p = 0.025$, $\eta_p^2 = 0.18$, and Target category × Target elongation × Shape congruency, $F(1, 26) = 5.88$, $p = 0.023$, $\eta_p^2 = 0.18$—indicating that prime shape indeed affected RTs in the shape-discrimination task. The three-way interaction was robust to the inclusion of more trials with long RTs when using the "mean ±3 SD" outlier definition, $F(1, 26) = 6.26$, $p = 0.019$, $\eta_p^2 = 0.19$, and we further explored it by testing the Target elongation × Shape congruency interaction separately for tool and animal targets (Figure 3). For tool targets, the two-way interaction was significant, $F(1, 26) = 4.30$, $p = 0.048$, $\eta_p^2 = 0.14$, because the Shape congruency effect was larger for elongated targets (589 vs. 600 ms) than for nonelongated targets, where it was numerically reversed (647 vs. 635 ms). Post hoc tests revealed that the facilitatory effect was significant, $t(26) = 2.15$, $p = 0.041$, while the reversed effect was not, $t(26) = -1.42$, $p = 0.166$. Using the "mean ±3 SD" outlier definition (Figure 3B), post hoc tests were significant for the facilitatory effect (606 vs. 623 ms), $t(26) = 2.10$, $p = 0.046$, and the reversed effect (682 vs. 661 ms), $t(26) = -2.14$, $p = 0.042$. For animal targets, the two-way interaction was not significant, $F(1, 26) = 0.09$, $p = 0.769$, $\eta_p^2 < 0.01$.

Finally, we observed a significant effect of Target elongation in the shape task because it took participants longer to respond to nonelongated targets as compared to elongated targets (626 vs. 604 ms), and this main effect was mainly driven by nonelongated tools.
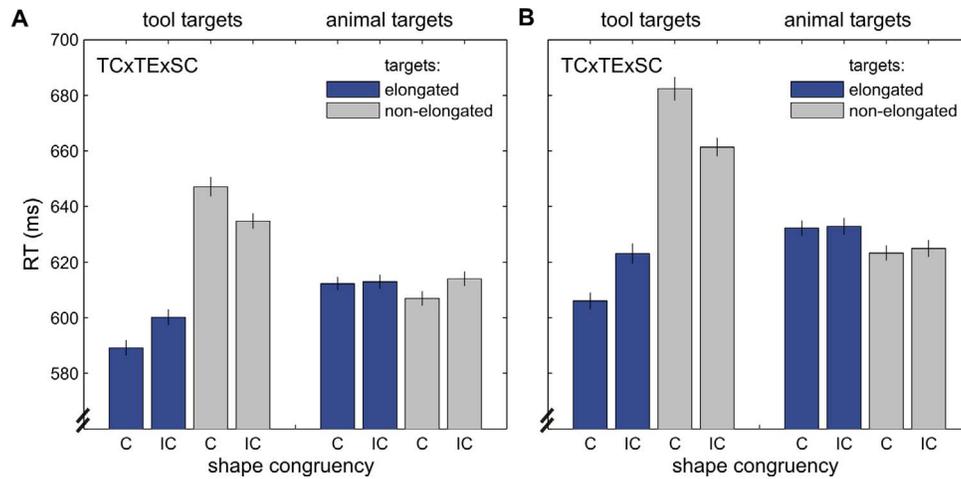
Figure 3. RTs in the shape task of Experiment 2. Plotted are RTs (in milliseconds) illustrating the Target category (TC) × Target elongation (TE) × Shape congruency (SC) interaction. (A) Analysis based on the interquartile range outlier definition by Tukey (1977). (B) Analysis based on the "mean ±3 SD" outlier definition, which included more trials with long RTs. Target stimuli were either tools or animals. Blue bars denote RT data from trials with elongated targets, and gray bars denote RT data from trials with nonelongated targets. Shape congruency of targets and primes was either congruent (C) or incongruent (IC), irrespective of category. Plotted are the mean ± Cousineau–Morey corrected error bars for within-subject designs (Cousineau, 2005; Morey, 2008).

Stimulus orientation

When preparing our stimuli, we aimed for an approximate matching of stimulus orientations between the two elongated categories. Due to the fact that the matching was only approximate (Supplementary Figure S2B), and since we randomly chose prime and target exemplars on each trial (with the exception that exemplars could not be identical), there was some variability of absolute differences between prime and target orientation across the experimental conditions (39°–51°; Table 3). Note that absolute orientation differences were defined to be within the range 0°–89°.

We reasoned that the visual processing of stimulus orientation might precede any higher level shape analysis, and that it thus could have influenced the results in the shape task.[2] Specifically, we focused our exploratory control analysis on the conditions with an RT effect involving elongated targets—i.e., the effect of shape congruency observed for tool stimuli but not for animal stimuli (indicated by blue bars in Figure 3). We limited the analysis to trials with elongated primes, and calculated Pearson correlation coefficients between absolute differences between prime and target orienta-

tion on the one hand and RT on the other hand separately for each participant. If stimulus orientation had a modulatory influence on the RT effect, then we should expect a difference between the coefficients for trials with tool targets and the coefficients for trials with animal targets. Coefficients turned out to be slightly larger for tool targets than for animal targets (tools: $r = 0.052$; animals: $r = -0.042$; two-sided paired t test), $t(26) = 2.13$, $p = 0.043$.

Familiarity and manipulability ratings

Average familiarity ratings for the four sets of stimuli (Supplementary Figure S1, subset) were as follows: elongated tools: 3.63; nonelongated tools: 3.88; elongated animals: 2.36; nonelongated animals: 2.70. An exploratory analysis of manipulability ratings (elongated tools: 4.42; nonelongated tools: 4.36; elongated animals: 2.13; nonelongated animals: 2.49) revealed that tools were rated as significantly more manipulable than animals, $F(1, 30) = 59.67$, $p < 0.001$, $\eta_p^2 = 0.67$; nonelongated stimuli were rated as slightly more manipulable than elongated stimuli, and the main

| | Prime | | | |
Target	Elongated tool	Nonelongated tool	Elongated animal	Nonelongated animal
Elongated tool	51 ± 1	43 ± 1	43 ± 1	46 ± 1
Nonelongated tool	44 ± 2	46 ± 1	44 ± 2	39 ± 1
Elongated animal	43 ± 1	43 ± 2	52 ± 1	43 ± 1
Nonelongated animal	47 ± 1	42 ± 1	44 ± 1	43 ± 1

Table 3. Absolute orientation differences between prime and target (mean ± SEM; °) in Experiment 2 across participants (N = 27).

effect of Shape turned out to be significant, $F(1, 30) = 5.13$, $p = 0.031$, $\eta_p^2 = 0.15$, as did the Category × Shape interaction, $F(1, 30) = 9.42$, $p = 0.005$, $\eta_p^2 = 0.24$, because shape influenced tool manipulability ratings less than manipulability ratings of animals.

Discussion

As in Experiment 1, we found no evidence supporting the notion of elongation-based unconscious priming in a category task, as proposed by Almeida et al. (2014). However, using the same stimuli and setup in the same group of participants, but with a shape-discrimination task (elongated vs. nonelongated) instead of category discrimination, the RT results from Experiment 2 provided some evidence for priming.

We found facilitatory priming by shape-congruent versus shape-incongruent primes for elongated tool targets, and a reversed (albeit not robust) RT difference for nonelongated tool targets. Or, put differently, we found that elongated primes could elicit faster shape discrimination of tool targets, elongated and nonelongated alike. Our RT data thus suggest that some shape information can still be extracted under CFS and affect manual target responses in a shape-discrimination task. Numerically, both effects were relatively small (11 and −12 ms) but well within the range of significant RT differences (8–12 ms) reported by Almeida et al. (2014). Our RT differences are also comparable with recently reported numerical priming effects under CFS (Hesselmann, Darcy, Sterzer, & Knops, 2015; Hesselmann & Knops, 2014). Two further studies, however, found no evidence for unconscious priming and suggest an even lower bound for priming effects under CFS (Izatt, Dubois, Faivre, & Koch, 2014; Peremen & Lamy, 2014).

From a broader perspective, our finding that prime shape can escape CFS suppression and affect subsequent manual responses to target stimuli appears to support the notion that interocularly suppressed stimuli are processed at the level of features and coarse feature configurations (Gayet et al., 2014). CFS is a method of interocular suppression and thus closely related to binocular rivalry, the mechanisms of which have been extensively investigated in the last decades (Blake & Logothetis, 2002; Sterzer, 2013). Although it is not yet clear whether CFS should be regarded as a variant of binocular rivalry that induces particularly strong suppression (Shimaoka & Kaneko, 2011), or whether CFS is supported by mechanisms distinct from binocular rivalry (Tsuchiya et al., 2006), a reasonable default view would be to expect only little high-level processing during CFS (Breitmeyer, 2014b), given the limited stimulus processing during binocular suppression (Blake, 1988; Cave, Blake, & McNamara, 1998;

Kang, Blake, & Woodman, 2011; Zimba & Blake, 1983). However, the current CFS literature sketches an increasingly fuzzy picture of the extent to which high-level unconscious visual processing is possible under CFS (Heyman & Moors, 2014; Sterzer et al., 2014; Yang et al., 2014). Future studies investigating low-level (e.g., shape priming) and high-level (e.g., category priming) effects under CFS should therefore aim to identify the relevant methodological differences between previous studies that might explain the heterogeneous results.

General discussion

In two experiments, we found no evidence in support of the hypothesis that elongated prime stimuli, unconsciously presented under CFS, facilitate the task of categorizing manipulable objects (i.e., category-by-shape priming). We did, however, observe that prime shape affects the shape discrimination of subsequently presented tool stimuli. In the following, we will discuss our results in the shape task, address the notion of a dorsal-stream processing bias under CFS, and outline the limitations of the current study.

Priming in the shape task

We found that shape-congruent primes differentially affected the shape-discrimination responses for elongated and nonelongated tool targets. This pattern of results is difficult to reconcile with a simple priming model based on shape congruency alone, and it merits further exploration.

From these data one may tentatively conclude that elongated stimuli facilitated the shape task for tool targets, elongated and nonelongated alike. While this is a pattern rather to be expected in the category task (in line with Almeida's category-by-shape priming hypothesis), it could potentially be generated in the shape task as well, when assuming a fast and automatic category-recognition process that influences target processing in the shape task (Fabre-Thorpe, 2011; Mouchetant-Rostaing, Giard, Delpuech, Echallier, & Pernier, 2000). Obviously, the question then remains why we did not observe exactly this pattern in the category task. Speculatively, the category task might have desensitized perceptual pathways related to the processing of prime elongation and thus diminished category-by-shape priming; by contrast, the shape task—requiring only attention to basic visual features—sensitized perceptual pathways and boosted category-by-shape priming. Attentional sensitization has previously been proposed as a mechanism to

explain enhanced and decreased priming effects observed under different task sets (Kiefer, 2012; Kiefer, Adams, & Zovko, 2012). According to this model, attentional sensitization of unconscious processing by task sets is achieved by enhancing the sensitivity of task-relevant pathways and reducing the sensitivity of task-irrelevant pathways (Kiefer & Martens, 2010).

Alternatively, our results in the shape task might be due to differences in stimulus orientation. To the best of our knowledge, only one previous CFS priming study directly addressed this issue (Sakuraba et al., 2012, experiment 5). They used differently oriented (0°, 45°, 90°, 135°) prime stimuli and found significant priming effects for elongated tool targets only when geometric lines were used as primes, not when other oriented stimuli (less elongated diamond shapes and nonelongated "Pacman" stimuli) were used. The authors concluded, "It is unlikely that the orientations of elongated shapes have a significant impact on the priming effects found in previous experiments" (p. 3952). Based on this conclusion, we did not expect significant effects of stimulus orientation in our experiments, but we nevertheless aimed for an approximate matching of stimulus orientation between our elongated stimulus categories (i.e., tools and animals). However, Sakuraba et al. (2012) did not report whether their shape-priming effect was further modulated by the orientation differences between primes and targets. We addressed this question in a control analysis that was limited to conditions with elongated stimuli. It revealed that the correlation between orientation differences and RT was larger for trials with tool targets than for trials with animal targets. We conclude that stimulus orientation might have modulated the results in the shape task, although more experiments (e.g., with a small set of discrete stimulus orientations) will be needed to better understand the magnitude and direction of this modulation.

Are priming effects observed under CFS mediated by the dorsal visual pathway?

In an influential fMRI study, Fang and He (2005) reported largely preserved neural activity in the dorsal visual pathway in response to CFS-suppressed images of tools, while activity in the ventral stream was fully suppressed. In the context of the duplex vision model (Milner & Goodale, 1995, 2006), the results of Fang and He were interpreted as evidence that CFS could be used specifically to "isolate" or "bias" dorsal visual processing—i.e., selectively disrupt conscious object identification mediated by the ventral stream while leaving nonconscious (possibly visuomotor) processes mediated by the dorsal stream intact (Lin & He, 2009).

We have recently published a review of the accumulated evidence in relation to this "dorsal CFS bias" and conclude that, given the currently available data, a dorsal processing bias under CFS cannot be assumed (Ludwig & Hesselmann, 2015). At the neural level, for example, follow-up fMRI studies did not confirm the finding of preserved dorsal activity under CFS (Fogelson, Kohler, Miller, Granger, & Tse, 2014; Hesselmann, Hebart, & Malach, 2011; Hesselmann & Malach, 2011), and showed that CFS-suppressed category information (face vs. house) could be decoded from cortex in the ventral stream (Sterzer et al., 2008).

As mentioned before, both Almeida et al. (2014) and Sakuraba et al. (2012) assume that their tool-priming effects originate from dorsal visual processes only. While the observed RT differences are interpreted as category-by-shape priming effects in the former study and as shape-priming effects in the latter, both studies exclusively used elongated tools as target stimuli. It is interesting to note that the tool stimuli used by Fang and He (2005) were also exclusively elongated (personal communication). Our recent fMRI study, however, does not support the notion that CFS-suppressed stimulus elongation (within the tool category) is preferentially processed in the dorsal visual pathway, since we found that both dorsal and ventral regions of interest were informative of stimulus shape, i.e., faces versus elongated tools (Ludwig, Kathmann, Sterzer, & Hesselmann, 2015).

A new and potentially promising avenue of research could be to directly investigate the dorsal- and ventral-stream contributions to the priming effects by systematically varying prime contrast and extracting contrast-response curves for the observed RTs (Breitmeyer, 2014a; Tapia & Breitmeyer, 2011). The contrast-response curves would then be compared to the known contrast-response functions for magno- and parvocellular cells (Kaplan & Shapley, 1986). This novel approach, however, faces two major challenges. First, the mapping between the magno- and parvocellular systems and the two visual pathways is not exclusive (Merigan & Maunsell, 1993; Skottun, 2014). Second, fitting nonlinear functions to RT effects with upper bounds of approximately 8–12 ms would require an enormous number of trials, given the noise in RT data.

Limitations

The post hoc examination of width/length ratios of stimulus exemplars in each category used in Experiment 2 showed that the distribution of ratios was broader in the case of nonelongated tools as compared to the other three categories (Supplementary Figure

S2). We assume that this broader distribution of width/length ratios resulted in the long RTs for nonelongated tools in the shape task (and perhaps also in the category task). One might conclude that priming effects in the shape task could also have been modulated by the width/length ratio, which was not modeled as a random effect in the statistical analysis. Therefore, future studies should further investigate the influence of the distribution parameters of width/length ratio distributions on shape-priming effects under CFS. On the other hand, previous CFS priming studies using tool and animal stimuli also differed with respect to these distributions (Supplementary Figure S2) and showed priming by shape congruency only, suggesting some robustness of priming to variations in width/length ratio distributions. Finally, in our experiments suppressed prime stimuli were also presented as fully visible target stimuli; thus it cannot be excluded that the observed priming effects might reflect consequences of stimulus-response mappings that can act at several levels (classification, decision, action) and potentially lead to facilitating and reverse RT effects (Henson, Eckstein, Waszak, Frings, & Horner, 2014; see also Kunde, Kiesel, & Hoffmann, 2003). One way of protecting priming effects against alternate interpretation as stimulus-response mapping effects would be to use naming tasks in combination with primes not included in the target stimulus set.

Conclusion

We found evidence for priming in a shape task, but no evidence for priming in a category task, when prime stimuli were rendered invisible using CFS. Our results are in line with the notion that the visual processing of CFS-suppressed stimuli is limited to the level of features and coarse feature configurations. The degree to which the priming effect in the shape task can be modulated by other low-level (e.g., stimulus orientation) and high-level (e.g., target category) information awaits further investigation.

Keywords: continuous flash suppression, interocular suppression, priming, dual-stream model, dorsal stream

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Footnotes

[1] For an up-to-date CFS reference list, please refer to http://www.gestaltrevision.be/en/resources/reference-guides/83-resources/reference-guides/343.
[2] We would like to thank one anonymous reviewer for raising this point.
[3] Data from our study can be found at https://figshare.com/s/f2dda499bac6eb229f8b.

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