

Attention-based perceptual learning does not affect access to awareness

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Visual information that is relevant for an observer gains prioritized access to awareness (Gayet, Van der Stigchel, & Paffen, 2014). Here we investigate whether information that was relevant for an extended duration is prioritized for access to awareness when it is no longer relevant. We applied a perceptual-learning paradigm, in which observers were trained for 3 days on a speed-discrimination task. This task used a stimulus consisting of two motion directions, of which one was relevant to the task and one irrelevant. Before and after training, we applied a motion-coherence task to validate whether perceptual learning took place, and a breaking continuous flash-suppression (b-CFS) paradigm to assess how training affected access to awareness. The results reveal that motion-coherence thresholds for the task-relevant motion direction selectively decreased after compared to before training, revealing that task-relevant perceptual learning took place. The results of the b-CFS task, however, reveal that access to awareness was not affected by task-relevant learning: Instead, detection times for motion undergoing CFS decreased, irrespective of its direction, after compared to before training. A follow-up experiment showed that the time to detect visual motion also decreased after 3 days without training, revealing that perceptual learning did not cause the general decrease in detection times. The latter is in line with results by Mastropasqua, Tse, and Turatto (2015) and has important consequences for studies applying b-CFS to assess access to awareness: Studies that intend to apply measurements involving b-CFS on

different testing days should consider that breakthrough times will dramatically decrease from pre- to postmeasurement.

Introduction

At any moment in time during waking we are aware of only of a subset of the information that enters through the senses. What aspects of the incoming information determine what enters our awareness and what does not? Or, put differently, what information is prioritized over other information in gaining access to awareness? In recent years, this question has been addressed using a paradigm called breaking continuous flash suppression (b-CFS; Jiang, Costello, & He, 2007). The b-CFS paradigm is an adaptation of continuous flash suppression (Tsuchiya & Koch, 2005), a method used to suppress a visual stimulus from awareness by presenting it to one eye while presenting a high-contrast dynamic stimulus to the other eye. In b-CFS, a target stimulus is initially suppressed from awareness by CFS, and the time it takes for the target to overcome suppression and become available for report then indicates to what degree the target stimulus has prioritized access to awareness. b-CFS has revealed several factors that determine whether visual information receives prioritized access (reviewed in Gayet, Van

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der Stigchel, & Paffen, 2014). Potent factors include the characteristics of the stimulus—for example, stimuli with higher contrast (Tsuchiya & Koch, 2005) or higher spatial-frequency content (Tsuchiya & Koch, 2005; E. Yang & Blake, 2012) break CFS faster than stimuli with lower contrast or spatial frequency—and stimulus familiarity—upright faces break suppression faster than inverted faces (Gray, Adams, Hedger, Newton, & Garner, 2013; Jiang et al., 2007; Zhou, Zhang, Liu, Yang, & Qu, 2010). In this study, we focus on a third factor that has been found to modulate access to awareness: the relevance that a stimulus has to the observer.

Several studies have argued that stimuli that are of relevance to an observer gain prioritized access to awareness—for example, faces with direct gaze are prioritized over faces with averted gaze (Chen & Yeh, 2012; Stein, Senju, Peelen, & Sterzer, 2011). In addition, fearful faces break through suppression faster than neutral (Gray et al., 2013; Stein & Sterzer, 2014; E. Yang, Zald, & Blake, 2007) or happy faces (Gray et al., 2013; Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009; E. Yang et al., 2007), and happy (E. Yang et al., 2007) and angry (Gray et al., 2013) faces break through more slowly than neutral faces. This difference in detection times between faces of different emotional valences arguably relies on cortical visual processing rather than subcortical emotional processing, as it has been shown to rely on high-spatial-frequency information (Stein, Seymour, Hebart, & Sterzer, 2014) and to be fully accounted for by visual characteristics such as face-to-mouth curvature (Stein & Sterzer, 2012). These findings challenge the notion that the emotional valence of the faces (and thereby their behavioral relevance) determines the degree to which the stimuli are prioritized for access to awareness. Recently, however, it has become apparent that stimuli that have no intrinsic relevance to the observer can, under certain circumstances, be prioritized for access to awareness. For example, a target (e.g., a colored disc) suppressed by CFS breaks suppression faster when it is relevant for a concurrent (memory) task (Gayet, Paffen, & Van der Stigchel, 2013; Gayet, van Maanen, Heilbron, Paffen, & Van der Stigchel, 2016b; Pan, Lin, Zhao, & Soto, 2014; van Moorselaar et al., 2017). This result indicates that a suppressed target that happens to share a relevant stimulus dimension with a stimulus that is held in working memory is released from suppression faster, and hence that it receives prioritized access to awareness. Furthermore, we have recently shown that a stimulus signaling threat breaks suppression faster than a stimulus that does not (Gayet, Paffen, Belopolsky, Theeuwes, & Van der Stigchel, 2016a). In the latter study, the target that was prioritized for access to awareness again had no intrinsic relevance; it was

merely a color that had been previously coupled (via a fear-conditioning paradigm) with receiving electric shocks. However, what remains unclear from this study is whether stimulus relevance can have an enduring effect on access to awareness. That is, does a stimulus dimension that was relevant to an observer for an extended period of time still receive prioritized access to awareness when it is no longer relevant?

To make a stimulus dimension relevant for behavior for an extended period of time, we applied a perceptual-learning paradigm. Perceptual learning refers to an improvement on a psychophysical task after repeated exposure to a specific stimulus (for reviews, see Fahle, 2005; Sagi, 2011; and Watanabe & Sasaki, 2015). Perceptual learning can be highly specific—to retinal location (Fahle, 2004; Fahle & Morgan, 1996; Karni & Sagi, 1991; Sowden, Rose, & Davies, 2002), contrast (Adini, Sagi, & Tsodyks, 2002; Yu, Klein, & Levi, 2004), spatial frequency (Fahle, 1994; Fiorentini & Berardi, 1980; Poggio, Fahle, & Edelman, 1992; Sowden et al., 2002), orientation (Fahle & Edelman, 1993; Fiorentini & Berardi, 1980; Poggio et al., 1992), texture (Karni & Sagi, 1991), and motion direction (Ball & Sekuler, 1982, 1987; Saffell & Matthews, 2003; Vaina, Belliveau, des Roziers, & Zeffiro, 1998)—although more recent studies have shown that learning can also generalize over stimulus properties (Ahissar & Hochstein, 1997; Harris, Glikhsberg, & Sagi, 2012; Jeter, Doshier, Petrov, & Lu, 2009; Z. Liu & Weinshall, 2000; R. Wang, Zhang, Klein, Levi, & Yu, 2012; X. Wang, Zhou, & Liu, 2013; Xiao et al., 2008; J.-Y. Zhang et al., 2010; T. Zhang, Xiao, Klein, Levi, & Yu, 2010). Important for the present purpose is that perceptual learning has been shown to be dependent on what is attended during training (Ahissar & Hochstein, 1993; Paffen, Verstraten, & Vidnyánszky, 2008; Vidnyánszky & Sohn, 2005). This crucial role of attention in perceptual learning has led some to suggest that perceptual learning is the result of enduring attentional inhibition of the untrained features (R. Wang et al., 2012; Xiao et al., 2008; G.-L. Zhang, Cong, Song, & Yu, 2013; J.-Y. Zhang et al., 2010; T. Zhang et al., 2010).

In the present study, we adapted the paradigm used by Paffen et al. (2008), who showed that attention-based perceptual learning affects binocular rivalry. Binocular rivalry occurs when different images are presented to the two eyes: Perception will start alternating between the two images (Blake & Wilson, 2010). In the training phase, lasting 3 days, observers performed a speed-discrimination task involving dots moving in two directions, of which one was attended (the direction was relevant for the task) and the other ignored (the direction was not relevant for the task). To assess the consequence of training, two experiments were performed 1 day before and 1 day after training: a binocular-rivalry and a coherence-threshold experi-

ment. The results showed that relevance had different consequences for perceptual learning in the two experiments. Compared to before training, coherence thresholds were lower for the relevant motion direction and unaltered for the direction that was not relevant. This result shows that training increased sensitivity for the relevant motion direction and that perceptual learning had occurred. Notably, perceptual dominance during binocular rivalry of the motion direction that was relevant during training was not boosted due to training. Instead, perceptual dominance of the motion direction that was *not* relevant during training was *decreased*. Paffen et al. interpreted the binocular-rivalry result as showing that (irrelevant) information that is strong enough to interfere with processing of the behaviorally relevant information gets more strongly suppressed with repeated exposure, implying that perceptual learning involves the enduring attentional inhibition of the untrained features (R. Wang et al., 2012; Xiao et al., 2008; G.-L. Zhang et al., 2013; J.-Y. Zhang et al., 2010; T. Zhang et al., 2010).

In the current study, observers were trained to discriminate between the speeds of a particular (relevant) motion direction, thereby ignoring a motion direction that was also present but not relevant to the task. Before and after training, a motion-coherence threshold and a b-CFS experiment were performed. To be specific, we measured motion-coherence thresholds and b-CFS detection times for task-relevant, task-irrelevant, and untrained motion directions before and after training. As in the study by Paffen et al. (2008), the motion-coherence threshold experiment served to validate that training led to perceptual learning: Again, coherence thresholds for the relevant motion direction were expected to be lowered after compared to before training. For the b-CFS experiment, we had two predictions (that are not mutually exclusive): First, if the motion direction that was relevant during the training phase led to prioritized access to awareness, b-CFS durations for that direction should decrease after compared to before training. Second, if the training again led to enduring inhibition of the task-irrelevant information, we expected the b-CFS durations of the irrelevant motion direction to increase after compared to before training.

Study 1: Does perceptual learning affect access to awareness?

Study 1 consisted of three experiments. Each observer started with a b-CFS and a motion-coherence experiment on Day 1. On Days 2 through 4, observers were trained on a speed-discrimination task. On the final day of the study, observers again performed the motion-coherence and b-CFS experiments.

Method

Observers

Twelve observers (five female, seven male) who were unaware of the aims of the study participated in all three experiments for a total of 6 hr in the course of 5 days. All observers had normal or corrected-to-normal stereoscopic vision and indicated having no (family) history of epilepsy or seizures. All observers gave informed consent. The study was conducted in accordance with the Declaration of Helsinki.

Apparatus and stimuli

The experiments were conducted on an Apple dual 2-GHz PowerPC G5 equipped with two linearized 22-in. Philips monitors ($1,152 \times 864$ pixels; 85 Hz) and an Apple keyboard. Stimuli were presented using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) executed in MATLAB (Release R2010a; MathWorks, Natick, MA). Displays were viewed dichoptically through a mirror stereoscope from a chin rest, keeping the viewing distance at 60 cm. Stimuli appeared on a uniform gray background with an average luminance of 78.5 cd/m^2 for the left and 91.2 cd/m^2 for the right monitor (measured directly on the monitor). To facilitate fusion, two large ($16.1^\circ \times 16.1^\circ$) identical frames of white noise (mean luminance of 53.4 cd/m^2 for the left screen and 61.3 cd/m^2 for the right screen) surrounded the presentation surfaces.

In all experiments, targets consisted of circular dots ($\pm 26 \text{ dots/deg}^2$) appearing within a circular (training and coherence experiments) or semicircular (b-CFS experiment) aperture of radius 1.1° (see Figures 1 and 2). Individual dots were 0.05° in diameter and moved with a baseline velocity of $3.2^\circ/\text{s}$ in one direction throughout one lifetime (which lasted 1 s); dots moving out of the aperture were wrapped around to the other side. Dot color was randomly distributed between a 25% and 75% white/black mixture with a luminosity of 42.5 and 121.7 cd/m^2 for the left and 49.5 and 143.1 cd/m^2 for the right screen. To keep stimulus parameters constant, all experiments were performed on two displays using a mirror stereoscope, presenting identical stimuli to each eye in all but the b-CFS experiment. In that experiment, one eye was presented with either a blank presentation frame or one of the targets moving within a semicircular aperture. In the other eye, CFS masks consisting of high-contrast noise flashed at a constant rate of 10 Hz. Individual masks were created by filtering pink ($1/f$) noise with a rotationally symmetric low-pass filter ($\sigma = 0.2$) and making the resulting image binary under high contrast.

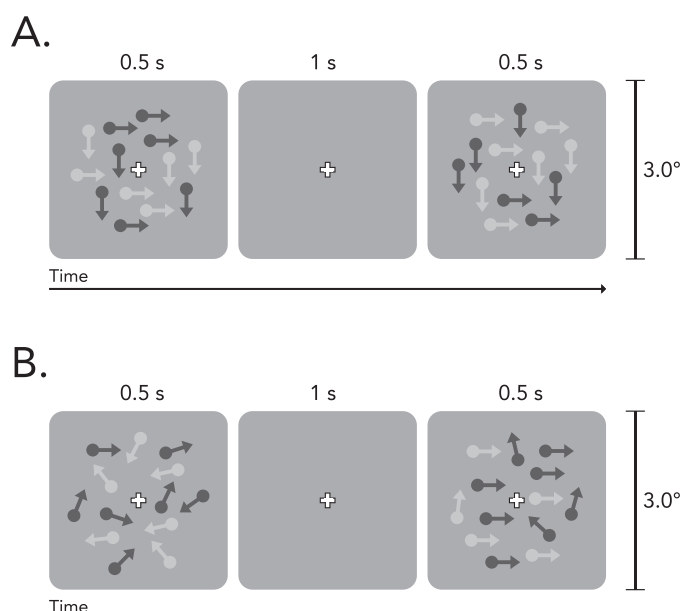


Figure 1. The stimulus used in (A) the training task and (B) the motion-coherence experiment. In the training task observers viewed two intervals, each containing two motion directions. For one of the motion directions, observers indicated which of the two intervals contained faster motion; for example, they indicated which interval contained faster rightward motion. A motion-coherence trial involved a two-alternative forced-choice task in which observers indicated which of two intervals contained coherent motion. The coherent motion was either rightward, downward, or left-upward.

General procedure

Observers performed in three experiments in the course of 5 days: 2 days of pre- and posttests (motion-

coherence and b-CFS experiments) and 3 days of training (training experiment). On Day 1, suppression durations were measured for dots moving downward, rightward, or left-upward using b-CFS. Also on Day 1, motion-coherence thresholds were estimated for all three directions at 80% accuracy. On Days 2 through 4, observers were trained in a speed-discrimination task involving two of the three aforementioned directions. Observers practiced discriminating the speed of dots moving in a specific (task-relevant) direction while concurrently being exposed to dots moving in another (task-irrelevant) direction. On Day 5, the experiments of Day 1 were repeated. On the days that involved the b-CFS and motion-coherence threshold measurements, the b-CFS measurement was performed first.

The experimental setup was broadly intended to mimic that of Paffen et al. (2008), with four notable differences: the presentation of feedback for the training and motion-coherence experiments; stereoscopic viewing for *all* procedures; the assignment into two relevance groups (rightward-as-relevant or downward-as-relevant); and the use of a single adaptive procedure for both training and threshold estimation.

Adaptive stimulus placement for the coherence and training experiments was controlled using accelerated stochastic approximation, or ASA (Kesten, 1958; Robbins & Monro, 1951). ASA is a nonparametric adaptive procedure that converges to any desired performance level. During training, ASA kept performance constant at 80%; in the pre- and posttests ASA was used for threshold estimation.

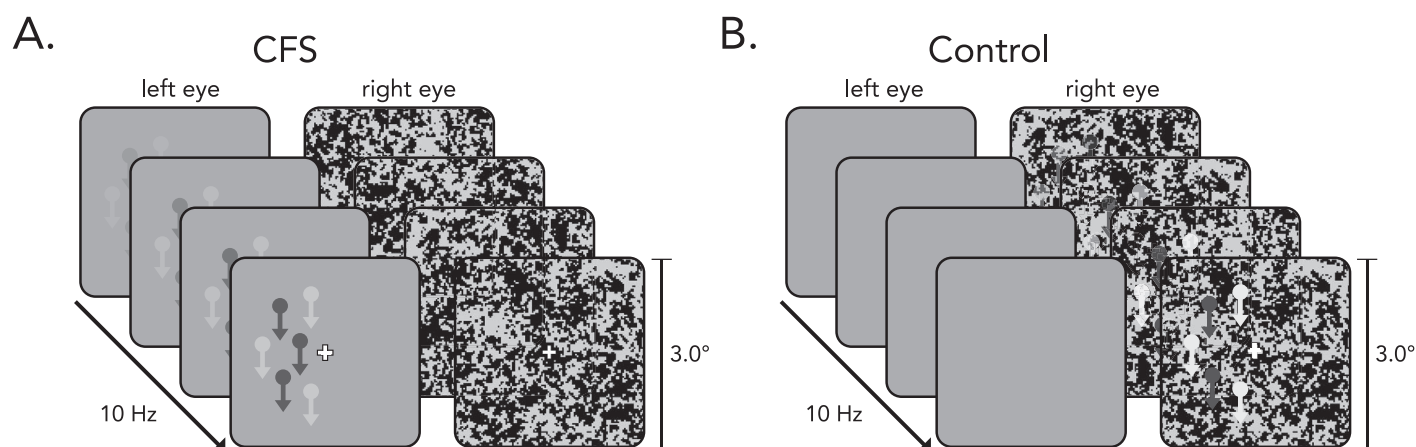


Figure 2. The stimulus sequence used in (A) the suppression condition and (B) the monocular control condition of the b-CFS experiment. (A) A series of high-contrast flickering masks was presented to one eye, while moving dots, gradually increasing in luminance, were presented to the other eye. Observers were instructed to press a button corresponding to whether the dots were on the left or right side of fixation. (B) The dots and masks were presented to the same eye, while the other eye was presented with the mean luminance background. The task was identical to that in the suppression condition.

Training experiment

On Days 2 through 4, observers performed in intensive training sessions involving two of the three aforementioned directions. In each trial, two dot clouds containing 50 rightward- and 50 downward-moving dots each were presented briefly (0.5 s), separated by a 1-s interstimulus interval. For six observers, the relevant direction was rightward; for the other six, the relevant direction was downward. In one interval, dots moved at $3.2^\circ/\text{s}$ in both directions. In the other interval, dots moved at $3.2^\circ/\text{s}$ in the task-irrelevant direction (e.g., downward), and slightly faster or slower in the task-relevant direction (e.g., rightward). Observers then had to indicate in which of the two clouds dots moving in the relevant direction were fastest.

Each training day consisted of five blocks. In one block, two interleaved ASA procedures of 80 trials each adjusted the speed contrast to keep performance constant at 80% correct. Feedback was provided both on a trial-by-trial basis (correct/incorrect) and at every 40 trials (current threshold estimate). To keep the observers motivated and engaged throughout the training, an additional monetary reward was distributed among the highest scoring observers. After 3 days, each observer had performed 2,400 trials.

Motion-coherence experiment

On Days 1 and 5, motion-coherence thresholds were estimated for all three motion directions. Observers were presented with two briefly presented dot clouds (0.5 s) separated by a 1-s interstimulus interval and had to indicate which one contained a global coherent motion direction. Coherence was adjusted by changing the percentage of dots moving in a specific direction. We estimated 80% correct thresholds by averaging the outcome of four interleaved ASA procedures for each direction. In each run, the coherence level was constrained between 1% and 50% coherence, starting at 25% and terminating when the lower step size reached 1.5% (i.e., 50–80 trials or 10 switches). In the pretest, feedback was presented both on a trial-by-trial basis (correct or incorrect) and after every 50 trials (current threshold estimate). Observers were encouraged to perform well and not to let their performance drop. To prevent observers from compensating potential training-induced direction-selective differences in performance, exact feedback was omitted from the posttest. Coherence thresholds for different directions were measured in separate blocks; testing orders were counterbalanced across observers and kept constant over pre- and posttest.

b-CFS experiment

On Days 1 and 5, b-CFS suppression durations were measured for all three motion directions. The procedure was embedded in a two-alternative forced-choice location-discrimination task. In each trial, a semicircular aperture containing 100% coherent moving dots appeared either right or left of the fixation cross (see Figure 2); observers indicated as fast and accurately as possible whether the target emerged left or right of fixation. We had two reasons for using this task. First, Gayet et al. (2013) showed that applying this procedure can be effective: In that study, observers indicated as fast as possible at what side of fixation a colored disc broke CFS, while at the same time maintaining an item in memory whose color either matched or mismatched the color of the b-CFS target. Even though the color was irrelevant for performing the b-CFS task, the results showed that matching colors broke suppression faster than mismatching colors. More importantly, however, we expected that if we asked observers to indicate the direction of motion of the target, they might develop a response bias towards the motion direction they had performed a task on extensively during training. To counter this possible bias, we decided to have observers report a feature orthogonal to the one they were trained on.

Three target types—random dots moving downward, rightward, or left-upward—appeared in two presentation conditions. In the experimental suppression condition, dots appeared gradually for one eye while being suppressed by CFS for the other eye (see Figure 2A). In the monocular control condition, targets appeared gradually on top of the masks for one eye while a blank presentation frame was presented to the other eye (see Figure 2B). The control monocular condition was intended to include all basic perceptual properties of the CFS condition except CFS suppression. If differences in suppression durations genuinely reflect differential selection for awareness (and not a difference in response time between stimulus conditions elicited after the interocular competition was resolved), effects should be visible only in the CFS condition (see Gayet et al., 2014). In both conditions, we made targets appear gradually by ramping the opacity from 0% to 100%; the steepness of the ramp was chosen so as to make the initial response times (RTs) approximately equal across conditions. For the suppression condition this meant that the target increased in opacity within 1 s; for the monocular condition, opacity increased within 2.5 s. RTs over 4 s were considered incorrect, and individual scores were computed by taking the median of all RTs. The two conditions (b-CFS and monocular control), three targets, and four locations (two for each eye, right or left of fixation cross) were randomly intermixed and counterbalanced in blocks of 24 trials, adding up to a total of 240 trials.

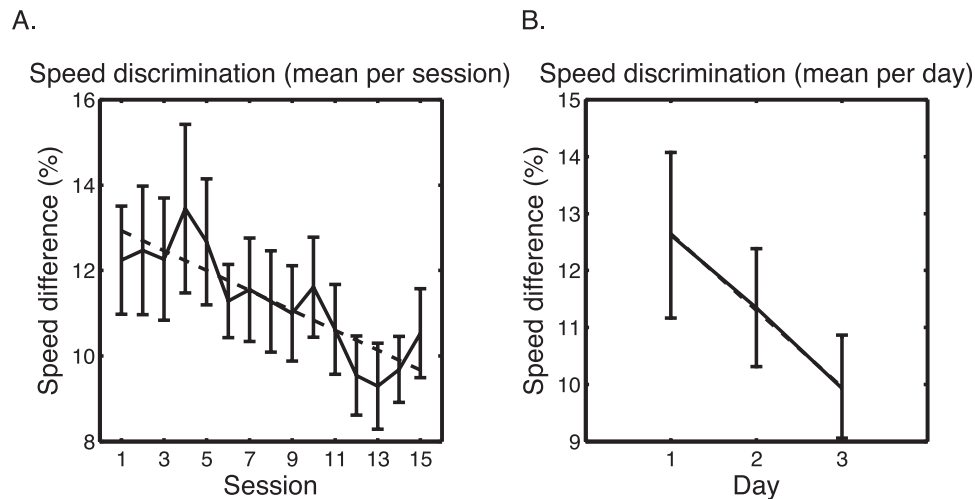


Figure 3. Performance in the training task. The left panel represents the mean improvement in speed discrimination over the 15 training sessions, reflected by a decrease in the percentage speed difference at which observers were 80% correct in reporting which of two intervals contained the fastest motion. Error bars represent 1 standard error of the mean. The dashed line represents the regression line, indicating the average improvement in speed discrimination over the course of the sessions. The right panel represents the improvement over the course of 3 days (with five sessions each); again, the dashed line represents the regression line and error bars represent 1 standard error of the mean.

Results

Analyses

Results were analyzed using repeated-measures ANOVAs, paired t tests, and linear regression. To assert whether the absence of significant effects reflected genuine null effects rather than a lack of experimental power, we also conducted Bayesian repeated-measures ANOVAs.

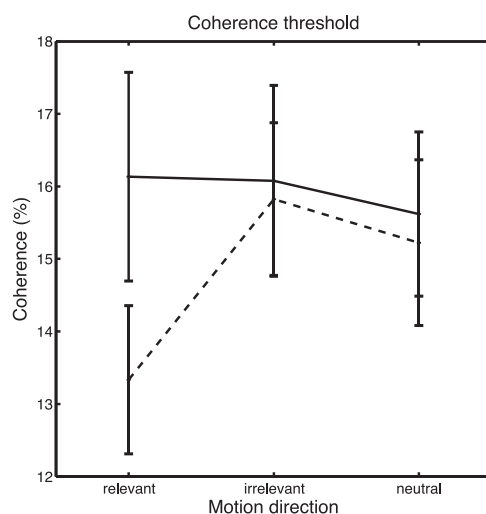


Figure 4. Results of the coherence-threshold experiment. The solid line represents coherence thresholds on Day 1 (before training); the dashed line, on Day 5 (after training). Error bars represent 1 standard error of the mean.

Training experiment

Training results are displayed in Figure 3. Individual scores reflect the (average) estimated threshold at various moments—that is, the (percent) difference in speed at which observers were 80% correct in reporting which of two intervals contained the fastest motion. Performing the training task led to an improvement during training. This is supported by a main effect of session number, $F(14, 154) = 3.18$, $p < 0.0001$, and by a significant negative slope of the regression line (Pearson's $\rho = -0.24$, $p < 0.001$). On average, observers improved 0.23% per session. We also analyzed the amount of improvement per day (Figure 3). There was a significant main effect of day, $F(2, 22) = 4.88$, $p = 0.018$, and a borderline significant negative slope of the regression line (Pearson's $\rho = -0.27$, $p = 0.052$). Observers improved on average 1.34% per day.

Coherence-threshold experiment

The results of the motion-coherence experiment are displayed in Figure 4. A repeated-measures ANOVA (with moment of testing and task relevance of the motion direction as within-subject factors) revealed a significant interaction between moment of testing (before versus after training) and task relevance, $F(2, 22) = 3.86$, $p = 0.036$. The main effect of moment of testing was borderline significant, $F(1, 11) = 4.73$, $p = 0.052$, while the main effect of task relevance was not significant, $F(2, 22) = 0.89$, $p = 0.42$. Notably, only the coherence threshold of the direction of motion that was

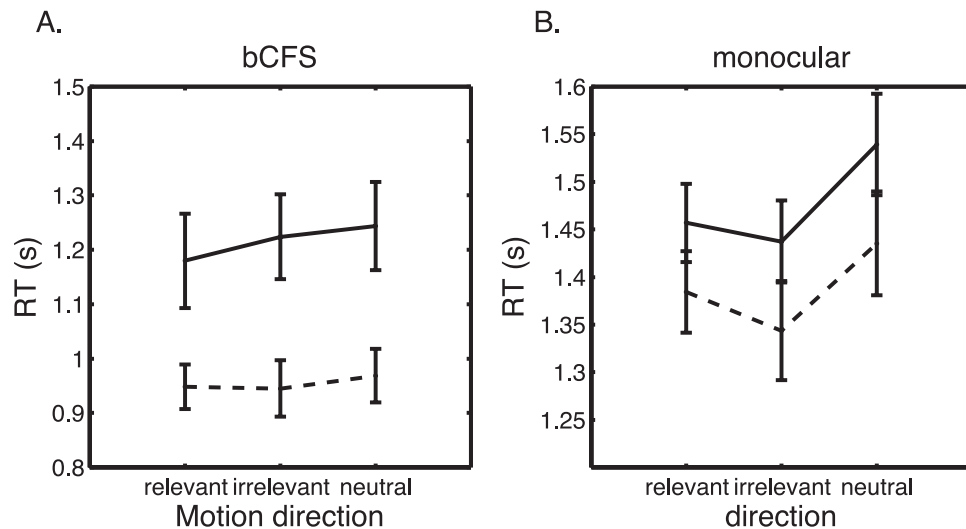


Figure 5. Results of the (A) b-CFS and (B) the monocular control experiment. The solid lines represent reaction times before training; the dashed line, after training. Error bars represent 1 standard error of the mean.

relevant during training was decreased after the training (paired t test before vs. after training), $t(11) = 2.72$, $p = 0.02$. There was no significant improvement for the thresholds of the other two motion directions, $t(11) < 0.79$, $p > 0.44$. Note that this result replicates that of Paffen et al. (2008).

b-CFS experiment

The results of the b-CFS experiment are displayed in Figure 5. A repeated-measures ANOVA (with factors moment of testing and task relevance of the motion direction) revealed a main effect of moment of testing, $F(1, 11) = 27.37$, $p < 0.0001$, but no significant main effect of task relevance, $F(2, 22) = 0.40$, $p = 0.68$, as well as no significant interaction, $F(2, 22) = 0.69$, $p = 0.51$. Pairwise comparisons for moment of testing for the three motion directions revealed that b-CFS durations for all three were significantly decreased, $t(11) > 3.56$, $p < 0.004$. Although the interaction was not significant, we also analyzed whether the decrease in b-CFS time was different for different motion directions. The amount of decrease did not differ between the three motion directions, $F(2, 22) = 0.69$, $p = 0.51$. These results reveal that there was no selective decrease in b-CFS time for the relevant motion direction, nor a selective increase in the b-CFS time for the irrelevant motion direction. Instead, all b-CFS times dropped by amounts that are not significantly different.

It could be argued that b-CFS was not selectively affected because the effect of training was relatively small (observers improved on average 1.34% per day). Perhaps we can reveal an effect of training on b-CFS for the observers with the largest improvement during training. To find out, we split the data in two based on the size of the learning effect for the 12 observers. The

six observers with the largest improvement during training improved by 5.24% from Day 1 to Day 3; the six observers with the smallest improvement improved by 0.13%. After this, we analyzed the effect of training on b-CFS in a repeated-measures ANOVA with moment of testing and motion direction as within-subject factors and amount of improvement on the training task (large vs. small) as a between-subjects factor. This analysis reveals a main effect of moment of testing, $F(1, 10) = 26.8$, $p < 0.001$, no main effect of motion direction, $F(2, 20) = 0.36$, $p = 0.70$, and no significant interaction between the two, $F(1, 10) = 0.67$, $p = 0.52$. The between-subjects factor was not significant, $F(1, 10) = 2.10$, $p = 0.18$. Importantly, none of the interactions between amount of improvement and the within-subject factors were significant, $F < 0.78$, $p > 0.40$.

As the improvement on the training task might have been variable across observers, it might be the case that the effect of training on b-CFS was not revealed by a repeated-measures ANOVA. For this reason, we tested whether the amount of increase in performance on the speed-discrimination task during training was related to the amount of decrease in RT in the b-CFS task. The results of this analysis reveal that there was no significant negative correlation between amount of improvement on the speed-discrimination task and amount of decrease in RT in the b-CFS task, for the relevant (Pearson's $r = -0.20$, $p = 0.26$), irrelevant (Pearson's $r = -0.24$, $p = 0.23$), or neutral (Pearson's $r = -0.26$, $p = 0.21$) motion direction. Thus, for all three motion directions, there was no correlation between amount of improvement on the speed-discrimination task and amount of decrease in RT in the b-CFS task.

The results of the monocular version of the experiment were similar. Here there was a main effect

of both time of testing (pre- vs. posttraining), $F(1, 11) = 9.61$, $p = 0.01$, and task relevance of the motion direction, $F(2, 22) = 17.53$, $p < 0.0001$. The interaction between them was not significant, $F(2, 22) = 1.58$, $p = 0.23$. The main effect of moment of testing refers to the fact that RTs were shorter after compared to before training (see Figure 5). The main effect of task relevance refers to the fact that RTs for the neutral motion direction were longer compared to those of the relevant ($p = 0.014$) and irrelevant ($p < 0.0001$) motion directions (irrespective of moment of testing). Again, the amount of decrease after training was not significantly different for the three motion directions, $F(2, 22) = 1.58$, $p = 0.23$.

We also analyzed whether the magnitude of the decrease in RT differed between the b-CFS and monocular conditions. For that purpose, we performed a repeated-measures ANOVA on the difference scores of the post- and pretests with viewing condition (b-CFS vs. monocular) and motion direction as factors. This analysis revealed a main effect of viewing condition, $F(1, 11) = 14.7$, $p = 0.003$, no main effect of task relevance, $F(2, 22) = 1.14$, $p = 0.34$, and no significant interaction, $F(2, 22) = 0.21$, $p = 0.91$. This analysis indicates that there was a difference in the magnitude of the decrease in RT between the b-CFS and monocular conditions: The decrease was larger in the b-CFS condition.

Finally, in order to assert whether the absence of a significant effect of task relevance in the b-CFS and monocular conditions reflected a genuine null effect rather than a lack of experimental power, we conducted a Bayesian repeated-measures ANOVA with the factors of viewing condition (b-CFS or monocular) and task relevance (relevant, irrelevant, or neutral) on the difference in RTs between the pre and post measurements. Following the suggestion of Dienes (2014), Bayes factors above 3 for any hypothesis were regarded as substantive evidence in favor of that hypothesis. Model comparisons revealed that all three models that included the factor of viewing condition were better at explaining the observed data than the null model (BF_{10} between 4×10^4 and 7×10^5), which in turn was six times better at explaining the observed data than the model that included only the factor of task relevance ($BF_{01} = 6$). The model that best explained the observed data included only the factor of viewing condition, and no main effect of or interaction with the factor of task relevance ($BF_M = 15$). From this, we conclude that the relevance of the motion direction did not impact access to awareness in the b-CFS task.

Discussion

Several conclusions can be drawn from the results of Study 1. First, training was effective: Observers'

performance on the speed-discrimination task improved steadily over the course of 3 days of training, reflected by the increasingly smaller speed differences they could discriminate. Second, training led to perceptual learning of the task-relevant motion direction: Coherence thresholds for the task-relevant motion direction were selectively decreased after compared to before training. Third, and most important to the goal of the present study, b-CFS durations of the motion directions were not selectively affected by the task relevance of the motion directions during training. Instead, RTs of the b-CFS (and the monocular) condition all decreased after compared to before training. Before discussing this result, we set out to test the possibility that the general decrease in b-CFS (and monocular) detection times was due to the 3-day training (where the training would have led to a nonselective improvement of the detection of either motion direction). For this, we repeated the b-CFS experiment, but now excluding the coherence experiment and the training sessions. Thus, observers performed only the b-CFS experiment on Days 1 and 5.

Study 2

Method

The stimulus, apparatus, and procedure for the b-CFS task (and the monocular control) were the same as for Study 1. Ten new observers participated in this experiment.

Results and discussion

We again performed a repeated-measures ANOVA (now with moment of testing and motion direction as factors). The results for the b-CFS experiment reveal main effects of moment of testing (pre vs. post), $F(1, 9) = 20.45$, $p = 0.001$, and of motion direction, $F(2, 18) = 14.43$, $p < 0.0001$, as well as a significant interaction between them, $F(2, 18) = 4.34$, $p = 0.029$. The interaction was caused by the decrease for rightward motion being borderline significantly different from the decrease for downward motion ($p = 0.098$, Bonferroni corrected), while the other differences were not significantly different. The main effect of direction was caused by rightward-motion detection times being significantly shorter than for the downward ($p = 0.001$) and left-upward ($p = 0.008$) motions.

The monocular control condition revealed main effects for moment of testing, $F(1, 9) = 44.08$, $p < 0.0001$, and direction of motion, $F(2, 18) = 10.94$, $p = 0.001$, but the interaction was not significant. Response

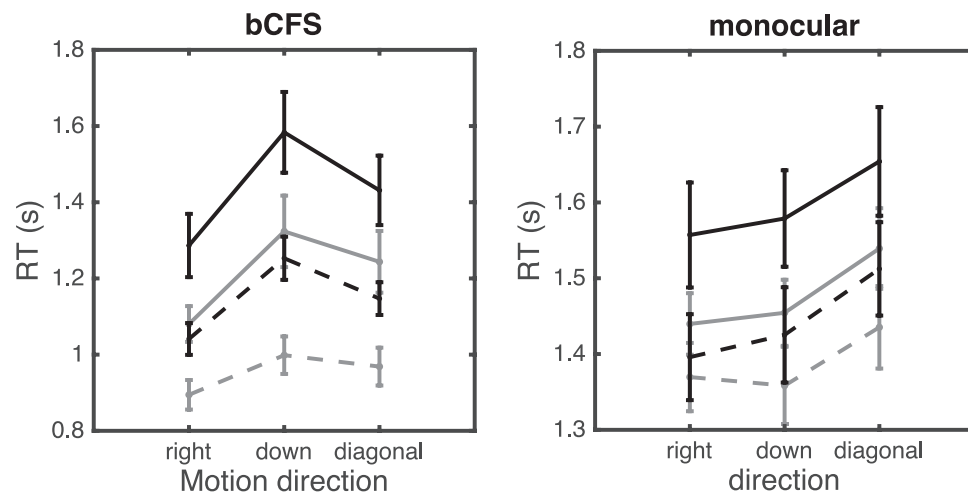


Figure 6. Results of (A) the b-CFS and (B) the monocular control experiment (Study 2). The solid black lines represent reaction times before training; the dashed black line, after training. The gray lines represent the results of the b-CFS and monocular conditions of Study 1. Error bars represent 1 standard error of the mean.

times were significantly higher for the left-upward motion compared to the rightward ($p = 0.001$) and downward ($p = 0.048$) motions.

Study 2 revealed, similar to Study 1, that RTs for the b-CFS and monocular viewing conditions dropped a-specifically after a pause of 3 days. As can be observed from the gray lines of Figure 6, the results of Study 2 are—apart from RTs being generally longer—highly similar to the results of the b-CFS and monocular conditions of Study 1. Notably, Study 2 excludes the possibility that being exposed to a motion-coherence threshold experiment and 3 days of training involving the same motion directions was responsible for the drop in RTs. Apparently, RTs for detecting motion during b-CFS and a monocular viewing condition decrease due to being repeated 3 days after initial exposure, irrespective of whether the motion directions are being presented in between. This result resembles those of a recent study by Mastropasqua, Tse, and Turatto (2015), which we discuss later.

General discussion

In the present study, we investigated whether a visual feature that was relevant to an observer for an extended period of time received prioritized access to awareness when it was no longer relevant. In order to answer this question, we applied a perceptual-learning paradigm similar to that of Paffen et al. (2008), in which observers were exposed to a task-relevant and a task-irrelevant feature (consisting of dots moving in a particular direction) during 3 days of training. Our results reveal that training led to perceptual learning: Observers gradually improved on the discrimination of

the speeds of a task-relevant motion direction. In addition, motion-coherence thresholds for the task-relevant motion direction were selectively decreased after compared to before training. However, even though perceptual learning of the task-relevant feature took place, the learning did not lead to increased prioritization for awareness of that feature: The time for which the task-relevant motion direction was suppressed by CFS did not selectively decrease after compared to before the learning took place. Instead of a selective decrease in b-CFS duration for the task-relevant motion direction, b-CFS durations for *all* motion directions (task relevant, task irrelevant, and neutral) decreased after compared to before training. Notably, this general decrease in b-CFS durations also occurred when observers were not exposed to the training sessions (Study 2). The latter finding excludes the possibility that the drop in b-CFS durations was caused by being exposed to 3 days of motion-discrimination training.

A conclusion that might be drawn from this study is that increased sensitivity for a visual feature does not lead to faster access to awareness for that feature. It might be the case, however, that this conclusion is limited to the specific stimulus used in the present study: The time it took to become aware of a certain motion direction did not change even though the threshold for detecting the motion direction decreased. It might be that the absence of transfer from the motion-coherence task to the b-CFS task is related to the specific task requirements of the two tasks: The motion-coherence task required an observer to detect the motion direction in one of the two intervals. Detecting at what location (left or right of fixation) moving dots become visible during CFS does not require the detection of motion direction: Whenever

dots become visible, an observer can do the task. That is, in the b-CFS task, location information suffices for performing the task at hand, whereas motion direction is imperative for performing both the motion-coherence and speed-discrimination tasks. This explanation makes sense when considering the results of Kiefer and Kammer (2017), who showed, using a masking paradigm, that information about the presence or absence of a stimulus is available earlier than information about the features of the stimulus. Thus, a possible reason for the absence of an effect of perceptual learning on b-CFS could be that increased sensitivity to a certain motion direction has nothing to aid in detecting (moving) dots that are suppressed by CFS, since the direction of motion would not yet be available at the moment of making a decision about the location of the dots.

As appealing as this interpretation might sound, it is in conflict with results from Gayet et al. (2013). In that study, observers indicated as fast as possible at what side of fixation a colored disc broke CFS, while at the same time maintaining an item in memory whose color either matched or mismatched the color of the b-CFS target. In their b-CFS task, similar to the present study, the identity of the target was irrelevant to the task: Observers merely indicated at what side of fixation the target broke CFS. Contrasting with our results, however, that study showed that relevant information *did* affect b-CFS durations. In sum, it remains unclear what determines when the identity of a target does or does not matter in performing a b-CFS task in which this identity is not relevant for the task.

Next to arguing that the training and b-CFS tasks involved different task requirements, it can be argued that processing of the motion stimuli used in the training and b-CFS tasks relied on different neural mechanisms, and that affecting a mechanism involved in the training task did not affect a different mechanism involved in processing the motion in the b-CFS task. Such an idea is not far-fetched, as it has been shown that coherent motion is processed at a different level than incoherent motion: Cai, Chen, Zhou, Thompson and Fang (2014) have shown that coherent motion is processed at the level of V3A, while incoherent motion is processed at the level of MT+. If we assume that our training stimulus contained incoherent motion, this logic could explain why b-CFS (which contained coherent motion) was not specifically affected by training. We think this explanation is unlikely for two reasons. First, our training stimulus was made up of two fully coherent motion directions (upward and downward), which is quite different from the incoherent stimulus used by Cai et al. In their study, the incoherent stimulus contained signal dots moving in a single direction, which were embedded in dots moving in random directions (i.e., noise dots). When we regard

the training stimulus as a coherent-motion stimulus, training on coherent motion *did* affect processing of incoherent motion in the present study (in the motion-coherence task). Second, Paffen et al. (2008) have shown that training using the same stimulus as the current study *does* affect processing of coherent motion: In their study, perception of fully coherent rivaling images was affected by training on the speed-discrimination task. Thus, even if we assumed that the training stimulus contained incoherent motion, that study would show that training on incoherent motion transferred to coherent motion (the binocular-rivalry stimulus).

Do our results have any impact on theories of perceptual learning? As outlined in the Introduction, perceptual learning can be highly specific (e.g., to retinal location, contrast, or spatial frequency) but can also generalize over stimulus features. In fact, the notion of generalizability has been central in a dispute between two theoretical accounts put forward to explain perceptual learning. According to the first, perceptual learning occurs due to changes in sensory representations of stimulus features. Such *representation modification* accounts propose that plasticity occurs in lower level visual areas that respond to basic features such as spatial frequency and orientation (Gilbert, Sigman, & Crist, 2001; Karni & Sagi, 1991; Lu, Yu, Watanabe, Sagi, & Levi, 2009). According to this account, a change in the sensory representation will be specific to the trained feature (e.g., by a sharpening of neural tuning of neurons sensitive to a trained orientation). This specific change in the sensory representation is responsible for the specificity that some studies observe.

On the other hand, *selective reweighting* accounts put forward that learning involves changes in the readout (at higher processing levels) of lower level stimulus features (Doshier & Lu, 1998, 1999; Jeter et al., 2009; J. Liu, Lu, & Doshier, 2010; Petrov, Doshier, & Lu, 2005; G.-L. Zhang et al., 2013). Here, learning is conceived as the selective reweighting of those channels that are most diagnostic in a particular task (e.g., discriminating between two orientations). In this account, perceptual learning is proposed to take place at a decision level instead of a lower sensory level. Potentially, our design would have been suitable for distinguishing between representation modification and selective reweighting: Using b-CFS, one can in principle infer whether a decision stage is involved in prioritization for awareness by comparing the results of the b-CFS experiment with a monocular condition. In a monocular condition, the CFS mask and target stimulus are presented to the same eye. If perceptual learning led to different b-CFS durations for trained versus untrained visual features, this difference could come about through a change in prioritization for awareness or a change in response

criterion (at a decision stage). A monocular condition could then distinguish between these two options: If a monocular condition revealed differences in response times similar to those of b-CFS conditions, the differences would have to be attributed to changes in response criterion. If, on the other hand, response times differed for the b-CFS condition but not for the monocular condition, the differences would not have to be attributed to changes in response criterion, but would reflect genuine changes in prioritization for awareness (see Gayet et al., 2014). The latter would indicate that increased sensitivity would come about not by selective reweighting (involving a decision stage) but by representation modification. Unfortunately, the present results do not allow us to distinguish between the two theoretical accounts: As we found no specific change in prioritization for awareness in the first place, we cannot use this reasoning to distinguish the two theoretical accounts.

The results are in part a successful replication of those of Paffen et al. (2008), as performing a speed-discrimination task on a task-relevant motion direction led to a specific improvement on a motion-coherence task for that direction of motion. Differently from Paffen et al., we do find a significant learning effect in the training task itself, while observers did not improve in the original study. There are at least three possible reasons why this study was successful in inducing a learning effect during training and the original study was not. First, it is known that feedback can facilitate learning (Ball & Sekuler, 1987), which explains why training was more effective in the present study. This argument can also be used to explain the difference between the present study and that by Saffell and Matthews (2003), who hardly found an improvement in speed discrimination after 7 days of training. Apart from other methodological differences, that study also did not present feedback during training. A second and related reason is that, contrary to Paffen et al. (2008), we distributed additional monetary rewards among the best performing observers, a prospect which may have helped to keep the observers motivated throughout the rather monotonous training. Third, Paffen et al. used the method of constant stimuli, sampling the speed difference from a predefined number of bins. Such a nonadaptive method is suboptimal when individual differences are large (making the task too difficult for some and too easy for others). Based on our data, the stimulus range used by Paffen et al. was rather large—varying between -50% and 50% . Using approximately the same stimuli, we found an initial 80% performance level at 12.6% velocity contrast. The task used by Paffen et al. may thus not have been very challenging, which reduces learning rates (Ahissar & Hochstein, 1997).

More relevant than the difference in performance on the speed-discrimination task is that Paffen et al. *did* find that binocular rivalry was affected by perceptual learning. In that experiment, dominance durations of the task-irrelevant motion direction were selectively decreased after training, indicating that the task-irrelevant motion direction became more efficiently suppressed. While we are not aware of other studies investigating the effect of training (or perceptual learning) on b-CFS, two recent studies have also shown that binocular rivalry is susceptible to training and learning. Dieter, Melnick, and Tadin (2016) trained observers by instructing them to attend a feature of one of two rivaling images while the image containing the feature was perceptually dominant. This training dramatically altered the predominance of the trained feature: After training, dominance of the attended image over the unattended image was increased compared to before training. It has also recently been reported that repeated exposure to an oriented grating that is suppressed by a high-contrast image presented to the other eye leads to decreased sensitivity for the suppressed orientation, assessed by measuring contrast-detection thresholds (Vergeer, Wagemans, & van Ee, 2016). The latter indicates that transfer from a task involving interocular conflict and a task that does not is bidirectional: Training transfers from a task not involving interocular conflict to one that does (Paffen et al., 2008), but it also transfers from a task that involves interocular conflict to one that does not (Vergeer et al., 2016). In sum, there are now three studies that show that binocular rivalry (that is, images containing interocular conflict) is susceptible to training or perceptual learning.

So why then does perceptual learning transfer to binocular rivalry but not to b-CFS? One possibility is that binocular rivalry and CFS are driven by different mechanisms. Two observations might support such a notion. First, suppression durations caused by CFS can last up to several minutes, which is much longer than those observed in binocular rivalry (Tsuchiya & Koch, 2005). Second, target suppression caused by CFS has been reported to be much stronger compared to binocular rivalry: Tsuchiya, Koch, Gilroy, and Blake (2006) reported that probe-detection thresholds for the suppressed eye were elevated by a factor of 3 during binocular rivalry, while thresholds went up by a factor of more than 20 for CFS. In spite of these two observations, recent evidence indicates that both phenomena are driven by similar, perhaps overlapping, mechanisms. For example, E. Yang and Blake (2012) reported that CFS masks consisting of only low spatial frequencies suppressed targets more strongly compared to masks consisting of only high frequencies. In addition, they found that there is a feature-selective suppression component to CFS (meaning that sup-

pression is stronger when features in the mask and target match). Both observations—spatial-frequency dependency and feature selectivity—mimic those reported for binocular rivalry, where both spatial-frequency dependency of suppression (e.g., Hollins & Hudnell, 1980; Y. Yang, Rose, & Blake, 1992) and feature selectivity (e.g., Stuit, Cass, Paffen, & Alais, 2009; Stuit, Paffen, van der Smagt, & Verstraten, 2011) have been reported. Recently, Han, Blake, and Alais (2018) showed that the influence of temporal-frequency content and the structure of (Mondrian) masks on suppression using CFS is also comparable to the influence on suppression induced by binocular rivalry. They found that spatial edges and low-temporal-frequency content are the driving forces in CFS, similar to their effects reported for binocular rivalry (e.g., Alais & Melcher, 2007; Levelt, 1965). Based on these observations, Han et al. concluded that suppression processes in CFS are similar to those involved in binocular rivalry.

If we assume that CFS and binocular rivalry are driven by similar or overlapping mechanisms, why was binocular rivalry affected in the present study and b-CFS was not? To get to an answer, we have to consider a difference between the two types of experiments. In a typical binocular-rivalry experiment (such as was applied by Paffen et al., 2008), the two conflicting images are perceived in alternation, whereby each image undergoes periods of perceptual dominance and suppression in alternation. As a result, any driving force that biases the perception of a particular image during binocular rivalry—such as attention (see Dieter & Tadin, 2011; Paffen & Alais, 2011), visual context (see Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004; Sobel & Blake, 2002), or perceptual learning—can exert its influence during perceptual dominance (when the image is consciously perceived) or during suppression (when the image is not consciously perceived). In contrast, in the b-CFS paradigm, where target images are initially suppressed, such a driving force can only affect detection times when the target image is still suppressed (and not yet consciously perceived). Along this reasoning, the present results suggest that perceptual learning of a task-relevant feature can affect the image when engaged in interocular conflict, but only when it is consciously perceived.

The final question to be answered is why the detection times of dot clouds in the b-CFS task dropped significantly when observers were presented with the same task, days after the initial exposure. Study 2 excluded the possibility that this drop was caused by repeated exposure to dot clouds in the speed-discrimination and motion-coherence experiments. This drop in detection times resembles the finding that the speed at which perception alternates during binocular rivalry increases with repeated exposure

(Suzuki & Grabowecki, 2007). A faster perceptual transition from the CFS mask to the moving dots would then resemble a faster switch rate for images engaged in binocular rivalry after repeated exposure. The results also resemble those of Mastropasqua et al. (2015), who reported that the chance of detecting a stimulus suppressed by CFS increases after repeated exposure with a single session. In that study, observers were instructed to detect a bar after a 3-s suppression by CFS in repeating blocks. In the present study, we also observed faster detection times for the monocular condition, indicating that a mechanism specific to resolving interocular conflict cannot account for the speeding we observed and can possibly also not account for the results of Mastropasqua et al. At present, we have no explanation for the shorter RTs after repeated exposure to b-CFS and the monocular condition, except that the speeding of RTs might have been caused by observers becoming more efficient in performing the task. Be that as it may, we do advise studies applying repeated exposure to b-CFS to take our results and those of Mastropasqua et al. into account. That is, studies that intend to apply multiple, consecutive measurements involving b-CFS on different testing blocks or days should take into account that breakthrough times will dramatically decrease from pre- to post measurement. This decrease can possibly obscure hypothesized effects of stimulus manipulations on b-CFS. This is especially relevant given the fact that differences in b-CFS durations between different conditions tend to decrease when overall response times become shorter (Gayet et al., 2016a; Gayet et al., 2016b; Gayet & Stein, 2017).

Keywords: perceptual learning, awareness, consciousness, motion perception, binocular rivalry

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