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Eye gaze adaptation under interocular suppression

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The perception of eye gaze is central to social interaction in that it provides information about another person's goals, intentions, and focus of attention. Direction of gaze has been found to reflexively shift the observer's attention in the corresponding direction, and prolonged exposure to averted eye gaze adapts the visual system, biasing perception of subsequent gaze in the direction opposite to the adapting face. Here, we tested the role of conscious awareness in coding eye gaze directions. To this end, we measured aftereffects induced by adapting faces with different eye gaze directions that were presented during continuous flash suppression, a potent interocular suppression technique. In some trials the adapting face was rendered fully invisible, whereas in others it became partially visible. In Experiment 1, the adapting and test faces were presented in identical sizes and to the same eye. Even fully invisible faces were capable of inducing significant eye gaze aftereffects, although these were smaller than aftereffects from partially visible faces. When the adapting and test faces were shown to different eyes in Experiment 2, significant eye gaze aftereffects were still observed for the fully invisible faces, thus showing interocular transfer. Experiment 3 disrupted the spatial correspondence between adapting and test faces by introducing a size change. Under these conditions, aftereffects were restricted to partially visible adapting faces. These results were replicated in Experiment 4 using a blocked adaptation design. Together, these findings indicate that size-dependent low-level components of eye gaze can be represented without awareness, whereas object-centered higher-level representations of eye gaze directions depend on visual awareness.

Keywords: eye gaze aftereffects, visual adaptation, visual awareness, interocular suppression, continuous flash suppression

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Introduction

Eye gaze provides an important source of information about another person's goals, intentions, and focus of attention (Allison, Puce, & McCarthy, 2000; Baron-Cohen, 1997; Itier & Batty, 2009; Nummenmaa & Calder, 2008). Throughout evolution, eye gaze has played a central role in social interaction and communication, both as mating and as threat signal (Emery, 2000). In the human visual system, eye gaze is processed with priority from the first days of life (Farroni, Csibra, Simion, & Johnson, 2002) and is capable of shifting attention in a relatively reflexive manner (Frischen, Bayliss, & Tipper, 2007). In the light of the outstanding significance of decoding eye gaze directions for adaptive behavior, here we asked whether specific directions of eye gaze can be processed without conscious awareness.

Studies on visual adaptation have provided important insights into the functional architecture of eye gaze coding in the human visual system. Prolonged exposure to an adapting face with averted gaze biases observers to categorize a subsequently presented test face with averted gaze in the adapted direction as looking straight ahead, whereas the categorization of a test face gazing in the opposite direction than the adapting face is virtually unaffected (Calder et al., 2007; Calder,

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Jenkins, Cassel, & Clifford, 2008; Jenkins, Beaver, & Calder, 2006; Schweinberger, Kloth, & Jenkins, 2007). Furthermore, compared to a baseline without adaptation, prolonged exposure to straight gaze results in a reduced tendency to categorize slightly averted gaze as pointing straight ahead, although this effect is weaker than the aftereffects induced by adaptation to averted gaze (Calder et al., 2008). The direction selectivity of eye gaze adaptation can be accounted for by a multichannel model of eye gaze representation, which holds that visual representations of eye gaze directions reflect the output of a three-channel system, with separate neural mechanisms coding left, straight, and right gaze directions (Calder et al., 2008).

In the present study, we tested whether gaze directions that were prevented from reaching visual awareness would induce direction-specific eye gaze aftereffects. To render adapting gaze directions invisible, we used continuous flash suppression (CFS; Tsuchiya & Koch, 2005), a potent interocular suppression technique in which a stationary stimulus presented foveally to one eye can be suppressed for a couple of seconds by a stream of continuously changing, colorful patterns flashed into the other eye. We have recently found that faces with direct gaze overcome CFS and break into awareness more quickly than faces with averted gaze, suggesting that information differentiating between direct and averted gaze is available to the visual system before conscious detection (Stein, Senju, Peelen, & Sterzer, 2011b). This "eye contact effect," however, could be mediated by a coarse subcortical face detection pathway that enables rapid awareness of faces with direct gaze (Senju & Johnson, 2009) and does not necessarily imply that the visual system unconsciously represents specific gaze directions that remain permanently invisible (Stein, Hebart, & Sterzer, 2011a).

Probing adaptation to stimuli rendered permanently invisible through interocular suppression provides a powerful means to trace the extent and limits of visual processing without awareness (Blake & He, 2005). Basic attributes of visual stimuli, such as orientation or translational motion can induce aftereffects despite interocular suppression (e.g., Bahrami, Carmel, Walsh, & Rees, 2008a, 2008b; Blake, Tadin, Sobel, Raissian, & Chong, 2006; Gilroy & Blake, 2005; Kanai, Tsuchiya, & Verstraten, 2006; Kaunitz, Fracasso, & Melcher, 2011; Maruya, Watanabe, & Watanabe, 2008; Moradi, Koch, & Shimojo, 2005; van Boxtel, Tsuchiya, & Koch, 2010). Most high-level aftereffects induced by more complex visual stimuli like faces, however, depend on visual awareness. In particular, high-level aftereffects of *invariant* facial features such as facial identity, face shape, age, or gender are eliminated when the adapting face is suppressed from visual awareness (Amihai, Deouell, & Bentin, 2011; Moradi et al., 2005; Shin, Stolte, & Chong, 2009; Stein & Sterzer, 2011).

Interestingly, however, adaptation to suppressed emotional facial expressions can result in significant aftereffects (Adams, Gray, Garner, & Graf, 2010; but see Yang, Hong, & Blake, 2010). One distinct aspect of facial expression is that it is a *changeable* (i.e., dynamical) facial feature. Changeable facial features such as facial expression, but also eye gaze, may be processed differently than invariant facial features such as face identity and gender. For example, in the model of Haxby and colleagues, changeable facial features (eye gaze, expression) are processed by the superior temporal sulcus (STS), even when these are presented as static pictures, while invariant facial features (identity) are processed by the lateral fusiform gyrus (Haxby, Hoffman, & Gobbini, 2000). Indeed, the STS has been found to respond more strongly to interocularly suppressed fearful than to neutral faces; whereas, no such difference was seen in fusiform gyrus activity (Jiang and He, 2006). Because both facial expression and eye gaze are processed by the STS (Allison et al., 2000; Calder et al., 2007; Haxby et al., 2000), it is conceivable that unconsciously processed eye gaze is also capable of inducing significant aftereffects. Alternatively, facial expression may be unique in inducing significant aftereffects under interocular suppression because of its emotional significance. For example, emotional expressions have been found to activate a subcortical pathway that bypasses visual cortex, a pathway that is less susceptible to interocular suppression (Jiang and He, 2006; Pasley, Mayes, & Schultz, 2004; Williams, Morris, McGlone, Abbott, & Mattingley, 2004).

Research on face adaptation aftereffects can also provide direct evidence for the dissociation between intact unconscious processing of simple stimulus features and abolished unconscious processing of more complex stimulus properties. For example, spatially distorted faces rendered invisible by CFS induce aftereffects only when the adapting and the test stimulus are displayed in the same size and to the same eye, suggesting that only monocular, low-level aspects of face shape adaptation can proceed without awareness, whereas representations of higher-level components of face shape depend on consciously perceiving the face (Stein & Sterzer, 2011). For one, these findings show that aftereffects from complex stimuli such as faces can reflect a combination of adaptation to low- and high-level properties and thus highlight the importance of controlling for low-level factors that may contribute to face adaptation aftereffects (e.g., Dickinson, Almeida, Bell, & Badcock, 2010). Moreover, such dissociations between the unconscious coding of stimulus properties of different complexity demonstrate that a systematic exclusion of potential low-level influences can reveal the role of visual awareness at different levels of the visual system, from monocular channels to size-invariant representations.

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In our present investigation we studied the role of visual awareness in eye gaze adaptation by systematically excluding potential low-level factors in a stepwise fashion in multiple experiments. In Experiment 1, we presented adapting and test stimuli in identical sizes and to the same eye. In Experiment 2, we presented adapting and test stimuli to different eyes to probe interocular transfer of eye gaze adaptation without awareness. Finally, in Experiments 3 and 4 adapting and test stimuli were displayed in different sizes to rule out the potential contribution of adaptation to low-level stimulus properties.

Experiment 1

In our main analysis we assessed eye gaze aftereffects induced by left and right gazing faces because previous studies on visible gaze directions obtained the largest aftereffects when observers were adapted to averted gaze directions (Calder et al., 2007, 2008; Jenkins et al., 2006). In these studies, eye gaze aftereffects were reflected in an increased tendency to categorize left and right test gaze directions as pointing straight ahead after adaptation to the same gaze direction (e.g., adapt left, test left), whereas no effect was found for test stimuli gazing in the opposite direction (e.g., adapt left, test right). Accordingly, in our main analysis we compared the proportion of participants' straight responses in *matching* trials, in which the gaze direction of the adapting and the test stimulus pointed in the same direction to *nonmatching* trials, in which the gaze directions of the adapting and the test stimulus pointed in opposite directions.

In support of the three-channel model of eye gaze representation, the study by Calder et al. (2008) indicated that the channel representing straight gaze is also adaptable. After adaptation to straight gaze observers categorized slightly averted gaze less frequently as looking straight ahead than in a baseline condition without adaptation. This aftereffect from straight gaze, however, was considerably weaker than from averted gaze and not all studies found significant aftereffects from straight gaze (Kloth & Schweinberger, 2010). We therefore investigated the effect of visual awareness on adaptation to straight gaze in an auxiliary analysis.

Method

Participants

Twelve participants (seven women, mean age = 26.2 years) took part in Experiment 1. In all experiments, observers had normal or corrected-to-normal vision and were naïve to the purpose of the study. The research protocol of all experiments adhered to the tenets of the Declaration of Helsinki.

Display and stimuli

Participants viewed a 19-inch CRT screen (1024 × 768 pixel resolution, 60-Hz refresh rate) from a distance of 50 cm through a custom-built mirror stereoscope, such that each eye was presented with approximately half of the screen. The participants' head was stabilized by a head-and-chin rest and stable binocular fusion was achieved through individual adjustment of the mirrors. A red frame (10.2° × 10.2°) containing additional fusion contours (width 0.8°, composed of random noise pixels) was presented to each eye. Stimuli were presented against a midgray background (30 cd/m^2) within these frames, with the remainder of the screen being black. A red fixation dot (0.7° × 0.7°) was displayed in the center of each frame and participants were asked to maintain stable fixation.

We created 10 facial identities as adapting stimuli and 10 different facial identities as test stimuli using FaceGen Modeller 3.1 (Singular Inversions, www.facegen.com), a software package widely used in research on face and gaze perception (e.g., Cristinzio, N'Diaye, Seeck, Vuilleumier, & Sander, 2010; Oosterhof & Todorov, 2008). For the adapting stimuli, we generated three gaze directions for each identity: maximally left (−100% in FaceGen), straight (0%), or maximally right (+100%). For the test stimuli, we generated seven gaze directions for each identity: −40%, −30%, −20%, 0%, +20%, +30%, and +40% (see Figure 1a). In a separate experiment, we determined the corresponding gaze angle for all gaze directions (see Appendix). A gaze direction of 100% deviation corresponded to approximately 31.6°, 40% to 14.8°, 30% to 11.1°, and 20% to 6.5°.

All faces were converted to grayscale, cropped to an oval shape (6.6° × 8.0°) that excluded external facial features, and equalized for mean luminance (30 cd/m^2) and global contrast (RMS contrast was set to 0.06). The edge of the face-enclosing oval was blurred into the background. To induce CFS, we generated high-contrast, multicolored Mondrian-like masks (8.4° × 8.4°) composed of randomly arranged circles, ovals, or diamonds. For each experimental block, a combination of one of these shapes with one of various color schemes was used.

Procedure

Before starting the experiment, we determined the participants' dominant eye either by a short experiment

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measuring the duration of perceptual suppression for each eye (the dominant eye being defined by shorter suppression durations, see Yang, Blake, & McDonald, 2010) or by the Miles test (Miles, 1930). A trial began with a 1-s presentation of the fixation dot only. Next, an adapting stimulus centered within the frame shown to the nondominant eye was gradually faded in by linearly increasing its contrast over 1 s, and then remained constant for another 5 s. In *suppression* blocks, CFS masks changing at 10 Hz were flashed into the dominant eye during this 6-s adaptation period. In *full dominance* blocks, the CFS masks were overlaid with a midgray oval corresponding to the size and shape of the adapting stimuli, such that no perceptual suppression was induced. Immediately following the adaptation period, the CFS masks and the fixation dot disappeared, and the adapting stimulus was replaced with a test stimulus displayed for 500 ms to the nondominant eye, followed by a 1.5-s presentation of the blank frames (see Figure 1b).

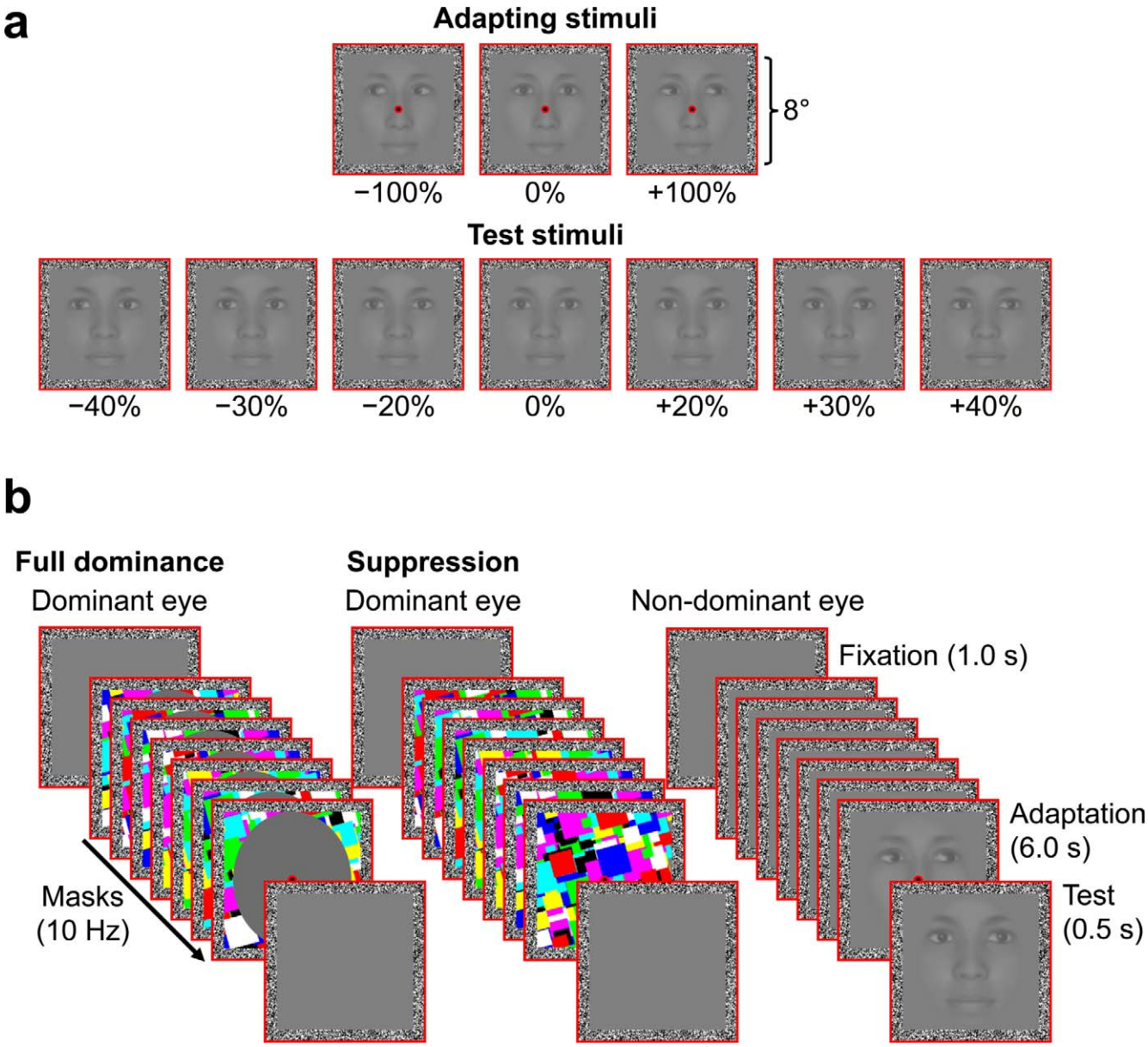

Figure 1. Sample stimuli and schematics of the procedure. (a) Examples of adapting stimuli (left gaze = −100%, straight gaze = 0%, right gaze = +100%) and test stimuli at all seven test gaze directions from maximally left (−40%) to maximally right (+40%). A separate experiment (see Appendix) showed that a gaze direction of 100% deviation corresponded to a gaze angle of approximately 31.6°, 40% to 14.8°, 30% to 11.1°, and 20% to 6.5°. (b) Schematics of example trials from Experiment 1. During the adaptation period, CFS masks were flashed at 10 Hz into the dominant eye, while an adapting stimulus was shown to the nondominant eye. In full dominance blocks, a gray oval overlaid on the CFS masks prevented perceptual suppression of the adapting stimulus.

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Participants categorized the test stimulus' eye gaze direction as left, straight, or right by pressing one of three arrow keys (left, down, right) on the keyboard with the right hand. We informed participants that response times would not be recorded and instructed them to be as accurate as possible. In suppression blocks, participants were additionally required to press the key "1" with the left hand when they saw any part of the adapting stimulus. At the end of a trial, a small question mark (0.7°× 0.7°) was shown for 1.7 s to give participants another chance to press "1" in case they had failed to report visibility during the adaptation period. We instructed participants to adopt a liberal response criterion and to press "1" even when they had only a vague idea of having seen any part of the adapting stimulus.

An experimental block contained 63 trials in which each combination of three adapting stimulus directions and seven test stimulus directions occurred three times. The identities of the adapting and test stimuli were selected at random for each trial and the trial order was randomized. Participants completed between 14 and 20 suppression blocks and between 7 and 10 full dominance blocks distributed over three to four 1.5-hr sessions on separate days. In addition, participants performed between four and eight baseline blocks that were identical to full dominance blocks, except for the exclusion of the adaptation period. Each session began with a baseline block. The order of the ensuing suppression, full dominance, and baseline blocks was randomized.

Results and discussion

Trials from the suppression blocks were classified according to the participants' reported visibility of the adapting stimulus as *partial suppression* (i.e., the adapting stimulus, or part of it, became visible) or *full suppression* (i.e., the adapting stimulus was invisible over the whole adapting period) trials. Across participants, the mean percentage of full suppression trials was 65.6% ($SD = 14.5\%$; see Supplementary Information Table S1 for the proportion of full suppression trials for all participants). For all analyses, we first analyzed responses separately for the three visibility conditions (full dominance, partial suppression, and full suppression).

Adaptation to averted gaze

Because we were not interested in differential effects for adaptation to left vs. right gaze (which actually have symmetrical effects, e.g., Jenkins et al., 2006), we collapsed trials across left and right adaptation conditions to increase the number of repetitions per cell. Thus, we compared *matching* trials with congruent adapting and test directions (both left or both right) to *nonmatching* trials with incongruent adapting and test directions (left-right or right-left) and did not analyze trials with straight test gaze directions (0% deviation), which were identical for matching and nonmatching trials. Adaptation was expected to result in an increased proportion of straight responses in matching trials.

Repeated measures ANOVAs with the factors trial type (matching, nonmatching) and test deviation (40%, 30%, 20%) on the proportion of straight responses revealed significant main effects of trial type for full dominance, $F(1, 11) = 29.35$, $p < 0.001$, partial suppression, $F(1, 11) = 20.07$, $p = 0.001$, and, most importantly, for full suppression, $F(1, 11) = 19.35$, $p = 0.001$. Thus, averted test gaze directions were categorized more frequently as pointing straight ahead after adaptation to the same gaze direction than after adaptation to the opposite gaze direction (see Figure 2a; for data from all individual participants, see Supplementary Information Figure S2). Eye gaze aftereffects were induced even by adapting stimuli that were fully suppressed. Not surprisingly, the proportion of straight responses increased with smaller test deviations, as reflected in significant main effects of test deviation for all visibility conditions, smallest $F(2, 22) = 73.06$, all $p < 0.001$. For none of the visibility conditions did the interaction between trial type and deviation reach significance, all $F(2, 22) < 2.34$, all $p > 0.120$.

Although fully suppressed adapting stimuli induced eye gaze aftereffects, this effect was smaller compared to partially suppressed adapting stimuli, as indicated by a significant interaction between visibility (partial suppression, full suppression) and trial type (matching, nonmatching), $F(1, 11) = 7.98$, $p = 0.017$. Thus, despite physical stimulation being constant, awareness of the adapting face increased the size of the aftereffect.

Adaptation to straight gaze

In this auxiliary analysis, we tested whether adaptation to straight gaze resulted in a reduced tendency to categorize averted test gaze directions as looking straight ahead. We compared the proportion of straight responses in straight adaptation trials (again pooled across left and right test directions) and baseline trials (Calder et al., 2008). An analysis of the proportion of straight responses in trials with straight test gaze directions (0% deviation) yielded no significant differences between baseline trials and trials with straight adapting stimuli from the three visibility conditions, largest $F(1, 11) = 1.48$, smallest $p = 0.250$. As in the

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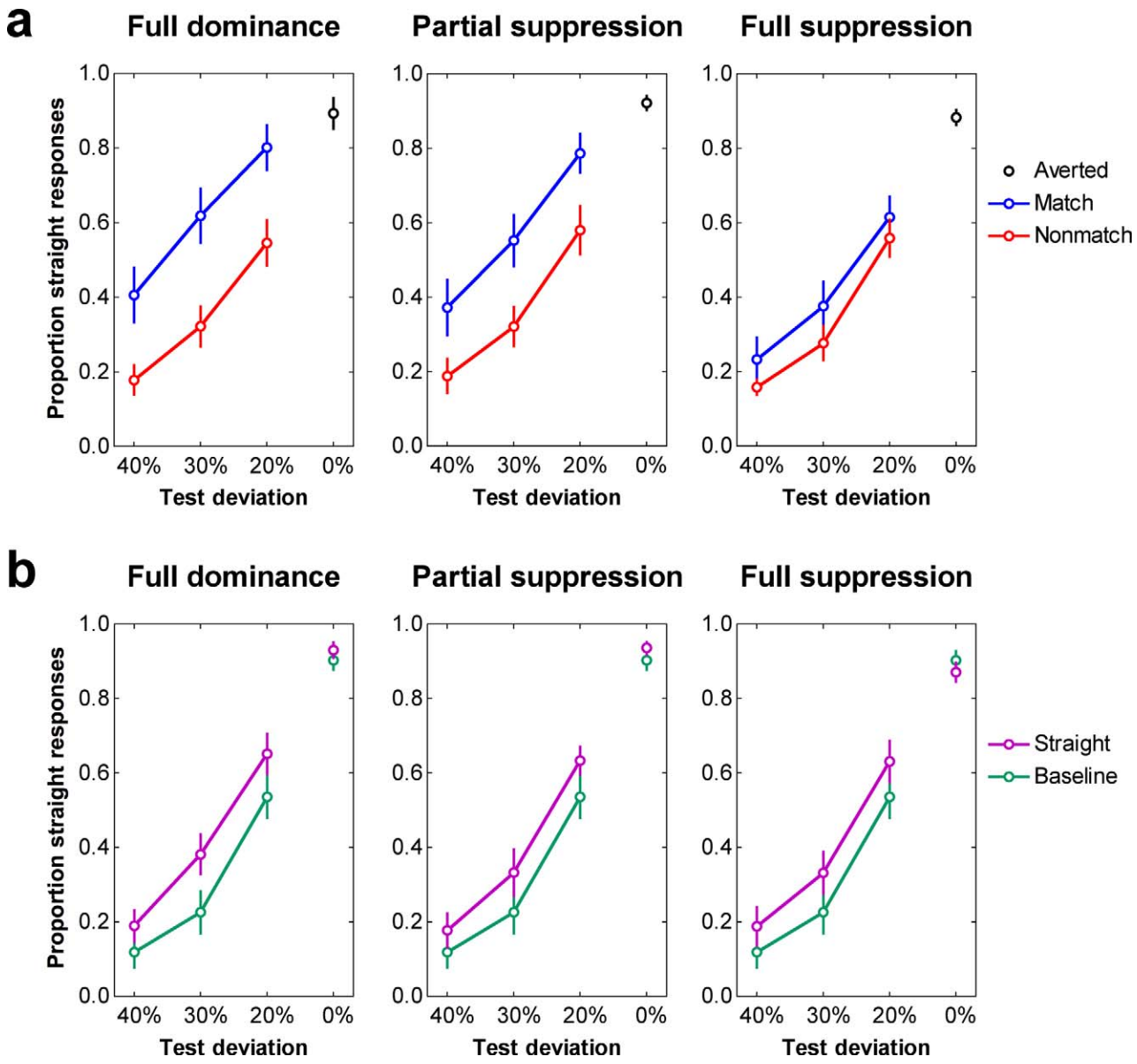

Figure 2. Results from Experiment 1. Separate panels show the mean proportion of straight responses as a function of test gaze deviation for full dominance, partial suppression, and full suppression trials. (a) Data from the analyses of adaptation to averted gaze directions comparing matching trials (i.e., adaptation to the same gaze direction as the test direction) to nonmatching trials (i.e., adaptation to the opposite gaze direction as the test direction). For straight test gaze directions (0% test gaze deviation) matching and nonmatching trials are the same and are plotted as adaptation to averted gaze. (b) Data from the analyses of adaptation to straight gaze, comparing straight adaptation trials to baseline trials. Please note that identical data from the baseline blocks with no adaptation are plotted in all panels. Error bars represent standard errors of the means.

main analysis, trials with straight test gaze directions were excluded from subsequent analyses.

Repeated measures ANOVAs with the factors trial type (adapt straight, baseline) and test deviation (40%, 30%, 20%) yielded significant main effects of trial type for all visibility conditions, smallest $F(1, 11) = 19.87$, largest $p = 0.001$. However, as can be seen from Figure 2b, contrary to our hypothesis adaptation to straight gaze resulted in a *higher* proportion of straight responses. The interaction between trial type and test deviation was significant only for full dominance, $F(2, 22) = 3.61$, $p = 0.044$, reflecting a larger difference for the 30% deviated gaze direction (see Figure 2b), but neither for partial suppression, $F < 1$, nor for full suppression, $F(2, 22) = 1.09$, $p = 0.353$.

Thus, for none of the three visibility conditions did this auxiliary analysis reveal eye gaze aftereffects from adaptation to straight gaze directions. Surprisingly, after adaptation to straight gaze participants more frequently categorized test stimuli as looking straight

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ahead than in the baseline condition with no adaptation. One possible reason for this discrepancy with previous reports (Calder et al., 2008) is that in our adaptation blocks all adapting directions were randomly intermixed to exclude carryover effects from partially suppressed to fully suppressed trials. Therefore, the channels coding left and right gaze may have been adapted to a certain degree throughout each block, thereby overshadowing the weaker effect of adaptation to straight gaze. We will return to this issue in Experiment 3.

In summary, Experiment 1 revealed adaptation to averted eye gaze to be reduced but not eliminated by CFS. However, because we presented adapting and test faces in identical sizes, it is possible that adaptation to low-level properties contributed to the aftereffects induced by fully suppressed adapting stimuli. In our previous research, we found that even interocular transfer of face adaptation can be eliminated by CFS (Stein & Sterzer, 2011; also see Maruya et al., 2008). Therefore, in Experiment 2 we first studied the extent of interocular transfer of eye gaze adaptation induced by visible and invisible adapting stimuli. In Experiment 3, we tested whether eye gaze aftereffects from invisible adapting stimuli persisted despite a size change between the adapting and the test stimulus, as has been shown for adaptation to visible eye gaze directions (Calder et al., 2008; Jenkins et al., 2006).

Experiment 2: method

Participants

Fifteen participants (nine women, mean age = 24.7 years) took part in Experiment 2. Two of these observers had participated in Experiment 1 before.

Display, stimuli, and procedure

Experiment 2 was identical to Experiment 1, except that we now presented the test stimulus to the dominant eye to probe interocular transfer of adaptation to the stimulus shown to the nondominant eye. In addition, to reduce monoptic forward masking from the CFS masks (Turvey, 1973), blank frames were displayed for 117 ms between the offset of the adapting stimulus and the onset of the test stimulus. Participants completed between 14 and 23 suppression blocks, 7–10 full dominance blocks, and 4–7 baseline blocks, spread over three to four 1.5-hr sessions on separate days.

At the end of the last session, 13 of the 15 participants were tested in three additional blocks in which we assessed their ability to discriminate the gaze direction of suppressed adapting stimuli. This control experiment was identical to the suppression blocks, except that observers discriminated the gaze direction of the adapting stimulus. Furthermore, for the control experiment test faces were scrambled by dividing the inner oval of each original test stimulus in 112 squares, which were then randomly recomposed (the luminance and contrast were adjusted to match the original test faces). We presented scrambled test faces to avoid interference from the test faces' gaze direction and in order to prevent participants from inferring the gaze direction of the adapting face from putative aftereffects.

Results and discussion

In the suppression blocks of Experiment 2, the mean percentage of full suppression trials was 57.9% (SD = 19.1%; see Supplementary Information Table S1 for the proportion of full suppression trials for all participants).

Adaptation to averted gaze

As in Experiment 1, repeated measures ANOVAs with the factors trial type (matching, nonmatching) and test deviation (40%, 30%, 20%) yielded significant main effects of trial type for full dominance, $F(1, 14) = 44.46$, $p < 0.001$, partial suppression, $F(1, 14) = 19.65$, $p = 0.001$, and, crucially, for full suppression, $F(1, 14) = 6.05$, $p = 0.028$. Thus, eye gaze aftereffects induced by fully suppressed adapting stimuli showed interocular transfer (Figure 3a; for data from all individual participants, see Supplementary Information Figure S3). The main effects of test deviation were significant, smallest $F(2, 28) = 59.80$, all $p < 0.001$. The trial type-by-test deviation interaction was significant only for full dominance, $F(2, 28) = 10.21$, $p < 0.001$, reflecting a smaller effect at the most extreme test deviation (see Figure 3a), but neither for partial suppression, $F(2, 28) = 1.32$, $p = 0.284$, nor for full suppression, $F < 1$.

Although even fully suppressed adapting stimuli generated aftereffects, awareness of the adapting stimuli again boosted the effects, as demonstrated by a significant interaction between visibility (partial suppression, full suppression) and trial type, $F(1, 14) = 6.11$, $p = 0.027$.

Discrimination of suppressed gaze directions

In the control experiment, we tested participants' ability to discriminate the gaze direction of suppressed adapting stimuli. For full suppression, participants'

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performance ($M = 35.7\%$ correct, $SD = 8.0\%$) was not significantly different from the chance level of 33% correct, $t(12) = 1.23$, $p = 0.243$, demonstrating that participants could not discern the gaze direction of subjectively invisible adapting stimuli. By contrast, for partial suppression, discrimination performance ($M = 57.4\%$ correct, $SD = 14.3\%$) was significantly above chance, $t(12) = 6.15$, $p < 0.001$. Repeating the analysis of adaptation to averted gaze for the participants tested in the control experiment also showed a significant main effect of trial type for full suppression, $F(1, 12) = 7.73$, $p = 0.017$. Thus, adaptation to specific eye gaze directions occurred in the absence of awareness of those gaze directions.

Adaptation to straight gaze

The results from our auxiliary analysis again failed to provide evidence for adaptation to straight gaze (see Figure 3b). For all visibility conditions, in straight adaptation trials even straight test gaze directions (0% deviation) were categorized more frequently as looking straight ahead than in baseline trials, smallest $F(1, 14) = 7.07$, largest $p = 0.019$. Furthermore, for full dominance the proportion of straight responses to the other test gaze deviations (40%, 30%, 20%) was significantly higher in straight adaptation than in baseline trials, $F(1, 14) = 6.59$, $p = 0.022$. There was a similar trend for partial suppression, $F(1, 14) = 3.56$, $p = 0.080$, whereas for full suppression there was no significant difference

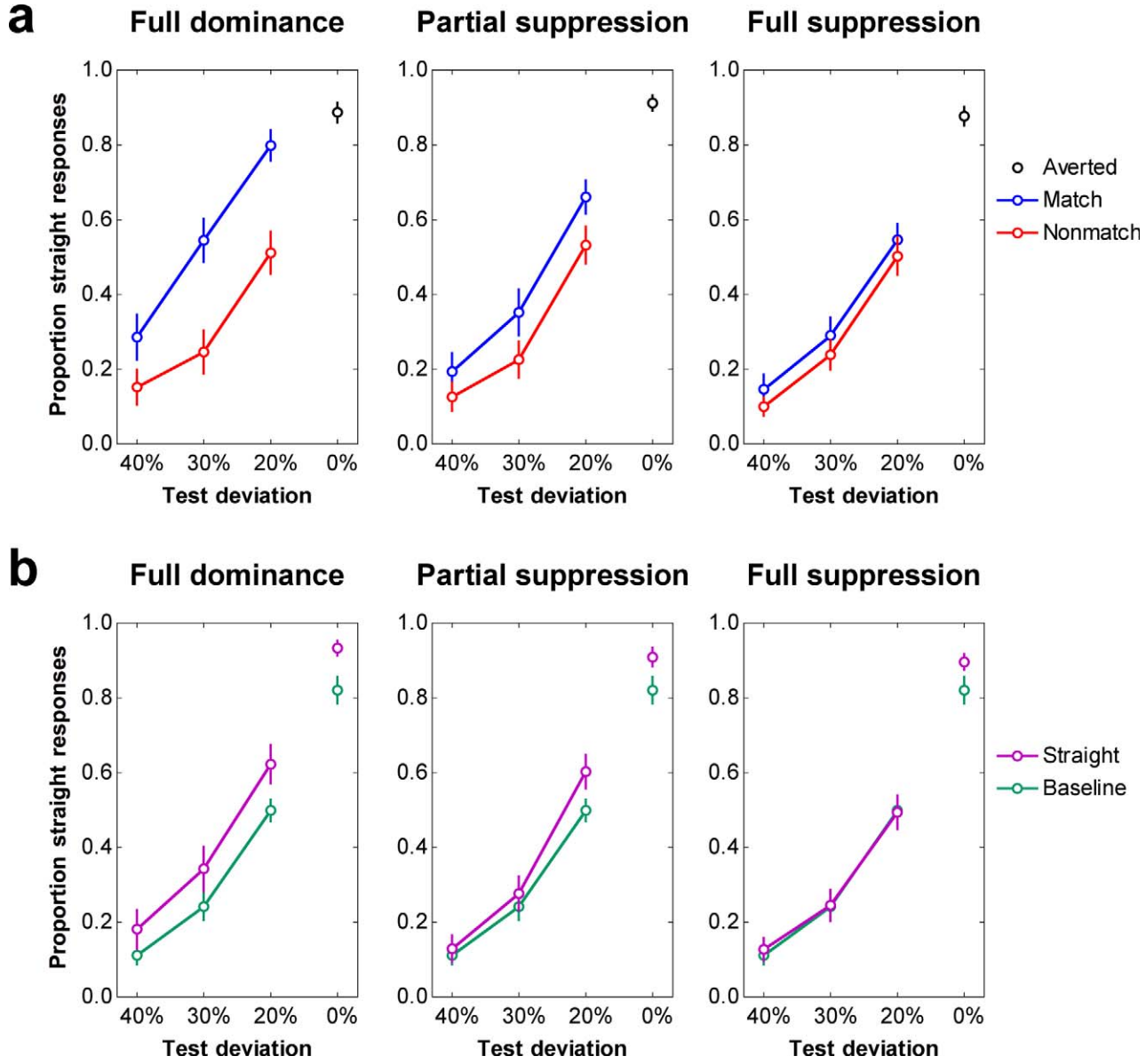

Figure 3. Results from Experiment 2. (a) Data from the analyses of adaptation to averted gaze directions. (b) Data from the analyses of adaptation to straight gaze. Error bars represent standard errors of the means.

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between straight adaptation and baseline trials, $F < 1$. Finally, the interaction between trial type and test deviation was significant for partial suppression, reflecting a larger difference for the 20% deviated gaze direction, $F(2, 28) = 5.07$, $p = 0.013$, but neither for full dominance, $F(2, 28) = 2.28$, $p = 0.121$, nor for full suppression $F < 1$.

Thus, while there was again no evidence for adaptation to straight gaze, Experiment 2 demonstrated interocular transfer of eye gaze aftereffects from invisible averted gaze directions. Nevertheless, because adapting and test faces were shown in identical sizes, it is possible that low-level adaptation contributed to these results. In Experiment 3, we therefore disrupted the spatial correspondence between the eye regions of the adapting and test stimuli by presenting them in different sizes (Calder et al., 2008; Jenkins et al., 2006).

Experiment 3: method

Participants

Eleven observers (seven women, mean age = 26.0 years) participated in Experiment 3. One of them had taken part in Experiment 2 before.

Display, stimuli, and procedure

Experiment 3 was the same as Experiment 1 (i.e., adapting and test stimuli were presented to the same eye), except that the test stimuli were reduced in size (5.0° × 6.0°) to eliminate any spatial overlap between the eye regions of the adapting and test stimuli. We replaced the straight gaze adaptation condition by a *blank* condition in which only the fixation dot and the CFS masks, but no stimulus, were shown during the adaptation period.

In three 1.5-hour sessions on different days, participants completed 14–23 suppression blocks, 7–10 full dominance blocks, and 4–7 baseline blocks. At the end of the third session, all participants were also tested in three control blocks in which we measured their ability to discriminate the gaze directions of suppressed adapting stimuli. The control blocks were designed as for Experiment 2, but contained 60 trials in which participants discriminated between two gaze directions only (left vs. right). In the control blocks, the blank condition was excluded.

Results and discussion

For trials from the suppression blocks with adapting stimuli (i.e., nonblank trials), the mean percentage of full suppression trials was 50.3% (SD = 13.8%; see Supplementary Information Table S1 for the proportion of full suppression trials for all participants).

Adaptation to averted gaze

For full and partial suppression, repeated measures ANOVAs with the factors trial type (matching, nonmatching) and test deviation (40%, 30%, 20%) again revealed significant main effects of trial type for full dominance, $F(1, 10) = 39.27$, $p < 0.001$, and for partial suppression, $F(1, 10) = 9.67$, $p = 0.011$. However, for full suppression there was no significant difference in the proportion of straight presses between matching and nonmatching trials, $F(1, 10) < 1$ (see Figure 4a; for data from all individual participants, see Supplementary Information Figure S4). Thus, eliminating the spatial overlap between the eye regions of the adapting and the test stimuli also eliminated aftereffects from invisible eye gaze.

The main effect of test deviation was significant for all visibility conditions, smallest $F(2, 20) = 55.96$, all $p < 0.001$. A significant interaction between trial type and test deviation for full dominance, $F(2, 20) = 4.83$, $p = 0.019$, reflected an increased effect for the 30%-deviated gaze direction. There was no significant interaction for partial suppression, $F(2, 20) = 1.04$, $p = 0.373$, and for full suppression, $F < 1$.

As in the previous experiments, a significant interaction between visibility (partial suppression, full suppression) and trial type showed that awareness of the adapting stimulus was associated with larger aftereffects, $F(1, 10) = 6.23$, $p = 0.032$.

Discrimination of suppressed gaze directions

In full suppression trials, participants' performance ($M = 50.7\%$ correct, $SD = 9.5\%$) was not significantly different from the chance level of 50%, $t < 1$. In partial suppression trials, by contrast, discrimination performance ($M = 74.6\%$ correct, $SD = 10.5\%$) was significantly above chance, $t(10) = 7.77$, $p < 0.001$.

Baseline vs. blank trials

Given the absence of evidence for adaptation to straight gaze in the previous experiments, in Experiment 3 we dropped the straight adaptation condition. Instead, the comparison between baseline trials with no adaptation to the blank condition from the adaptation blocks allowed us to test whether the proportion of straight responses was generally increased in adaptation blocks, perhaps because our mixed design some-

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what adapted the channels for right and left gaze throughout each adaptation block. Indeed, as can be seen from Figure 4b, compared to baseline trials, straight test gaze categorizations were more frequent in blank trials in both full dominance, $F(1, 10) = 10.73$, $p = 0.008$, and suppression blocks, $F(1, 10) = 5.63$, $p = 0.039$.

Thus, in the previous experiments a certain degree of constant adaptation of the left and right channels may have overshadowed adaptation to straight gaze. Critically, if both channels were adapted somewhat, this could have decreased our sensitivity for measuring a difference between matching and nonmatching trials and could thus have contributed to the null effect for full suppression in Experiment 3. To exclude this possibility, in Experiment 4 we adopted a blocked adaptation protocol in which participants were adapted to either left or right gaze throughout a whole block of trials.

Experiment 4: method

Participants

For Experiment 4, we selected six participants (three women, mean age = 27.2 years) who showed particu-

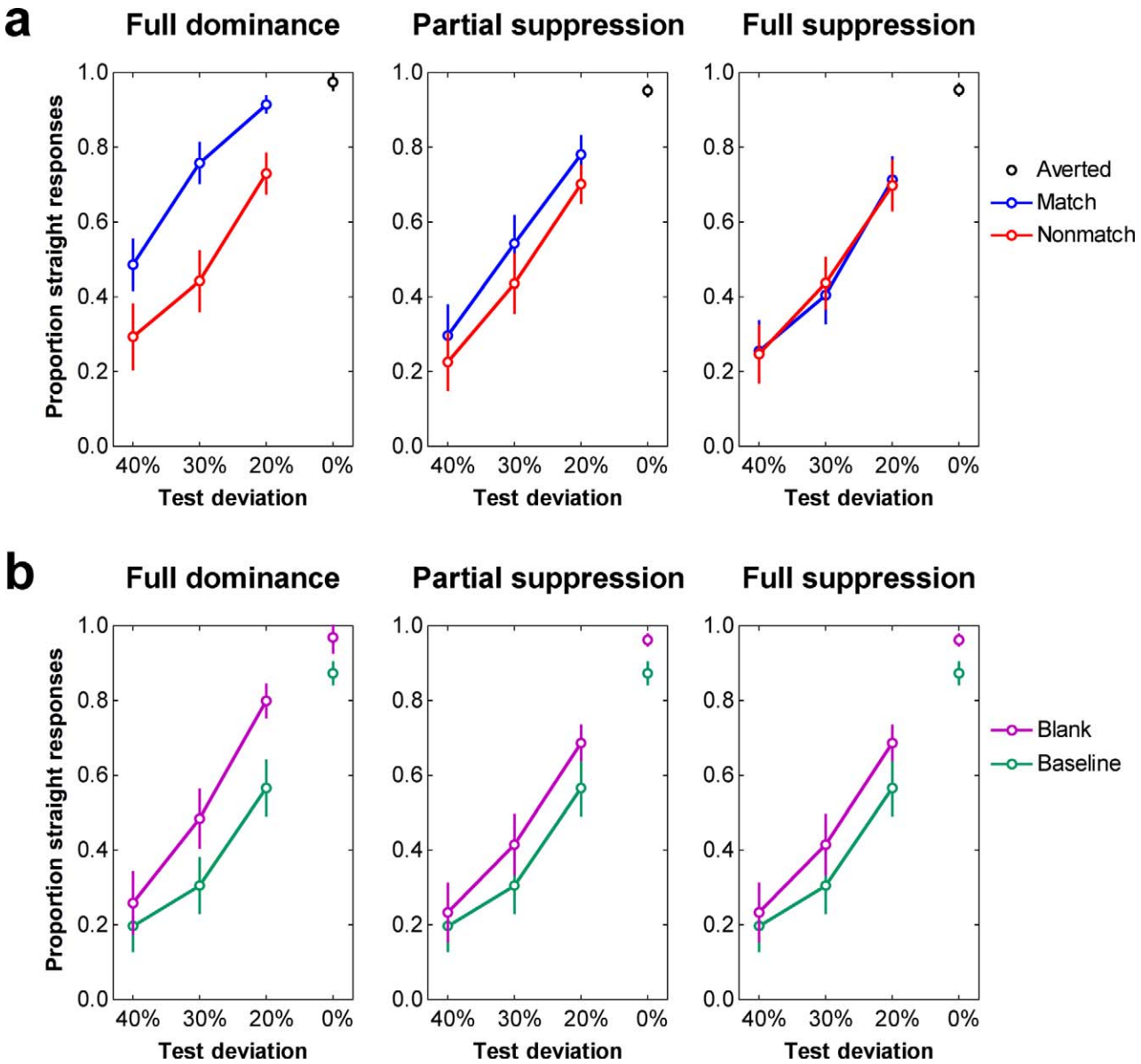

Figure 4. Results from Experiment 3. (a) Data from the analyses of adaptation to averted gaze directions. (b) Data from the analyses of baseline vs. blank trials. Please note that identical data from the blank trials in suppression blocks are plotted in the partial suppression and the full suppression panel. Error bars represent standard errors of the means.

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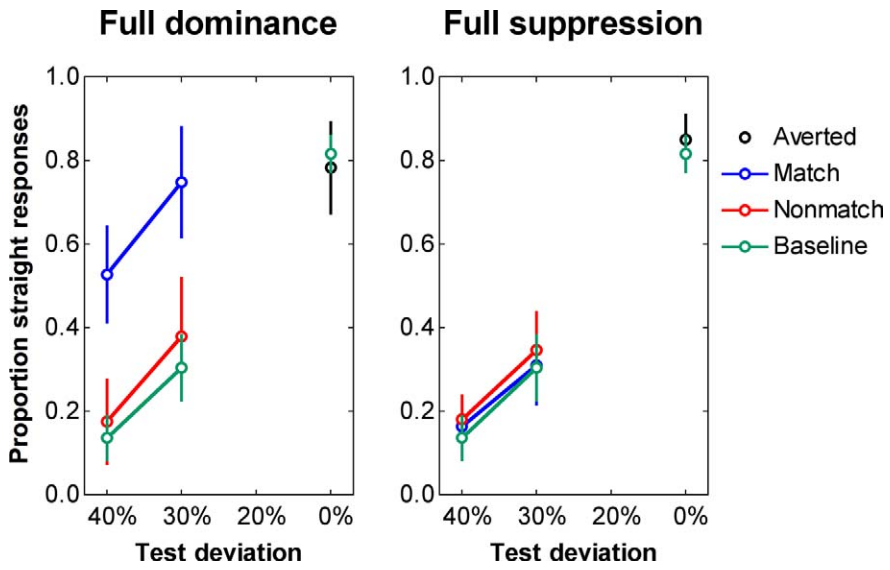

Figure 5. Results from Experiment 4. Please note that identical data from the baseline trials are plotted in the two panels. Error bars represent standard errors of the means.

larly robust perceptual suppression in other studies from our laboratory. Four of them had also participated in one of the previous experiments before.

Display, stimuli, and procedure

The display, the stimuli and the procedure of single trials were the same as in Experiment 3 (i.e., adapting and test stimuli were shown to the same eye). However, the implementation of a blocked adaptation protocol led to a number of changes in the experimental design. For each block, the gaze direction of the adapting stimulus (left or right) was selected at random and remained constant throughout the block. Full dominance blocks comprised 100 trials in which each of five test gaze directions (we excluded the 20% deviation condition) was shown 20 times and the face identities were randomly sampled. Suppression blocks were the same but ended as soon as observers indicated visibility of any part of an adapting stimulus. We analyzed only the trials preceding the trial in which the adapting stimulus became visible for the first time. The analysis of full dominance trials was matched accordingly. We analyzed only trials 1 to n from the full dominance blocks, where n was the mean number of trials in suppression blocks for a given participant. To prevent carryover effects (see Kloth & Schweinberger, 2008), blocks were separated by breaks lasting approximately ten minutes.

Participants completed two baseline blocks, two full dominance blocks, and 7–16 suppression blocks in three 1.5-hr sessions on separate days. Across participants, the mean number of trials in suppression blocks was 54.9 (SD = 31.2; see Supplementary Information Table S5 for the number of full suppression trials for all participants). At the end of the last session, there were two control blocks that were identical to those in Experiment 3.

Results and discussion

Adaptation to averted gaze

For full dominance, a repeated measure ANOVA with the factors trial type (matching, nonmatching) and test deviation (40%, 30%) yielded a significant main effect of trial type, $F(1, 5) = 19.99$, $p = 0.007$, reflecting an increased proportion of straight responses in matching trials. By contrast, for full suppression the main effect of trial type was not significant, $F < 1$, meaning that fully suppressed adapting stimuli again failed to induce eye gaze aftereffects (Figure 5; for data from all individual participants, see Supplementary Information Figure S6). The main effects of test deviation were significant for both full dominance, $F(1, 5) = 17.24$, $p = 0.009$, and full suppression, $F(1, 5) = 10.39$, $p = 0.023$, and there were no significant interactions, both $F < 1$.

Discrimination of suppressed gaze directions

In fully suppressed trials, participants' performance in discriminating left vs. right gazing adapting stimuli ($M = 52.8\%$ correct, $SD = 4.9\%$) was not significantly

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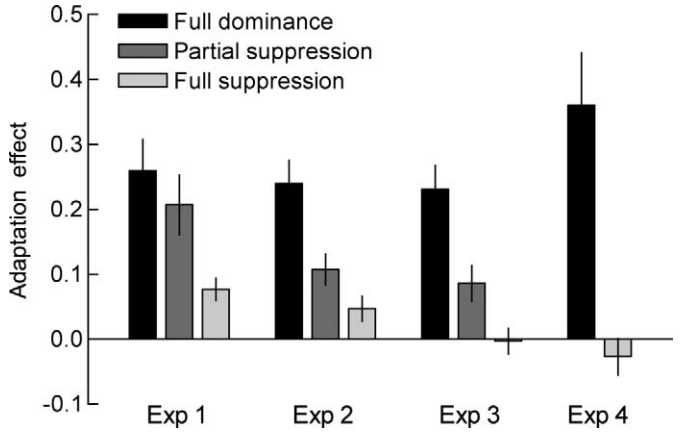

Figure 6. Eye gaze aftereffects from adaptation to averted gaze for all experiments. Bar plots show the mean adaptation effect, i.e., the mean difference in the proportion of straight responses between matching and nonmatching trials averaged across all test deviations (for Experiments 1–3: 40%, 30%, 20%; for Experiment 4: 40%, 30%). Error bars represent standard errors of the means.

different from the chance level of 50% correct, $t(5) = 1.40$, $p = 0.219$.

In summary, Experiment 4 again showed that invisible adapting stimuli failed to induce eye gaze aftereffects when they were presented in different sizes than the test stimuli, even with a blocked adaptation design. Thus, when the possibility of adaptation to low-level stimulus properties is ruled out by disrupting the spatial correspondence between the eye regions of the adapting and test stimuli, eye gaze aftereffects depend on visual awareness of the adapting stimulus.

Adaptation to averted gaze: comparison between experiments

Finally, we compared the size of eye gaze aftereffects from adaptation to averted gaze between experiments to quantify the degree of interocular transfer (Experiment 2 vs. Experiment 1) and size-invariant adaptation (Experiment 3 vs. Experiment 1). To this end, for each participant, we computed the *adaptation effect* as the mean difference in the proportion of straight responses between matching and nonmatching trials across all test deviations (40%, 30%, 20%), separately for full dominance, partial suppression, and full suppression (i.e., the adaptation effect corresponds to the respective main effect of trial type; Figure 6).

Interocular transfer (Experiment 2 vs. Experiment 1) did not significantly reduce the adaptation effect for full dominance ($t < 1$, mean difference in adaptation effects [MD] = 0.02, standard error of the difference [SED] = 0.06) nor for full suppression ($t(25) = 1.11$, $p = 0.277$, $MD = 0.03$, $SED = 0.03$). For partial suppression, there was a trend towards a significantly reduced adaptation effect ($t(25) = 2.03$, $p = 0.054$, $MD = 0.10$, $SED = 0.05$).

Size-invariant adaptation (Experiment 3 vs. Experiment 1) significantly reduced the adaptation effect for partial suppression ($t(21) = 2.20$, $p = 0.039$, $MD = 0.12$, $SED = 0.06$) and for full suppression ($t(21) = 3.01$, $p = 0.007$, $MD = 0.08$, $SED = 0.03$), but not for full dominance ($t < 1$, $MD = 0.03$, $SED = 0.06$). Thus, only under CFS were eye gaze aftereffects significantly reduced by introducing a size change between the adapting and the test face.

General discussion

We investigated the role of visual awareness in the coding of eye gaze directions in the human visual system. For this purpose, we measured aftereffects from adapting faces with different gaze directions presented under strong interocular suppression induced by CFS. Due to stochastic variations in the depth of interocular suppression (e.g., Blake & Logothetis, 2002), the adapting stimulus became visible in some trials and remained completely invisible in others, thus allowing us to assess the effect of visual awareness despite physical stimulation being constant.

Our main findings relate to adaptation to averted gaze and can be summarized as follows. First, when the adapting and the test stimulus were presented in identical sizes, we obtained aftereffects from subjectively invisible adapting stimuli, with larger aftereffects when the adapting stimulus became at least partially visible (Experiments 1 and 2). Second, in contrast to our previous findings on face shape aftereffects (Stein & Sterzer, 2011; also see Maruya et al., 2008) these aftereffects from invisible eye gaze survived interocular transfer (Experiment 2), meaning that information about invisible gaze directions can be represented at levels of the visual system beyond purely monocular channels. Third, introducing a size change between the adapting and the test stimulus abolished aftereffects from invisible eye gaze (Experiments 3 and 4), indicating that size-invariant eye gaze representations depend on visual awareness. Together, these findings suggest that size-dependent low-level properties of eye gaze directions can be processed without awareness, whereas size-invariant high-level representations of eye gaze directions are intimately tied to conscious awareness.

In addition to adaptation to averted gaze, one previous study also found aftereffects from straight

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gaze (Calder et al., 2008). By contrast, in the present Experiments 1 and 2 we did not find evidence for adaptation to straight gaze, irrespective of whether the adapting face was visible or suppressed. How could we account for this discrepancy? First, aftereffects from straight gaze are considerably weaker than aftereffects from averted gaze (Calder et al., 2008) and have not always been observed (Kloth & Schweinberger, 2010). One possibility is that the mixed adaptation protocol of Experiments 1 and 2 in which adapting stimuli with straight and averted gaze were randomly intermixed was less sensitive to detect the smaller aftereffect from adaptation to straight gaze than the more powerful adaptation protocol used by Calder et al. (2008) in which participants were adapted to one gaze direction for 2 min and subsequently received additional top-up trials containing adapting stimuli of the same gaze direction. Second, because adaptation to averted gaze is stronger than adaptation to straight gaze, in our mixed adaptation protocol adaptation from averted gaze trials may have carried over to straight adaptation trials and could thus have overshadowed the effect of straight adaptation. Indeed, in Experiment 3 the proportion of straight responses was increased in blank trials that were interleaved in the adaptation blocks but did not contain an adapting stimulus compared to trials from baseline blocks without adaptation, suggesting that the channels for averted gaze were adapted to a certain degree throughout the adaptation blocks. Third, aftereffects from straight gaze are restricted to small test deviations. While Calder et al. (2008) observed a reduction of straight responses after adaptation to straight gaze for a test deviation of 5°, no such effect was found for a test deviation of 10°. As the smallest test deviation of the present experiments corresponded to a slightly larger gaze angle (approximately 6.5°), our test stimuli may have not been optimal to measure aftereffects from straight gaze. Clearly, future studies are necessary to systematically investigate under which conditions aftereffects from straight gaze can be observed.

For adaptation to averted gaze, by contrast, we obtained robust aftereffects, enabling us to examine the role of visual awareness in the representation of eye gaze directions. Aftereffects from invisible adapting gaze directions presented in the same size as the test stimuli could reflect the unconscious extraction of geometrical or luminance cues from the eyes of the adapting stimulus. Although the facial identity always changed from the adapting to the test stimulus, there was still a substantial degree of spatial overlap between the eye regions of the two stimuli. Thus, it is conceivable that simple edge detection mechanisms sensitive to geometrical information from the eye regions that may be used to decode gaze directions, such as the position of the iris relative to the sclera together with the location of the corner of the eye within the face (e.g., Anstis, Mayhew, & Morley, 1969), were adapted without visual awareness. Another, not mutually exclusive possibility is that the pronounced luminance differences between the iris and the sclera (that may also constitute an important cue to infer gaze directions; e.g., Ricciardelli, Baylis, & Driver, 2000) resulted in negative afterimages and thereby shifted the perceived gaze direction of the test stimulus (Ando, 2002). These putative low-level mechanisms are consistent with orientation-selective visual adaptation (Bahrami et al., 2008a, 2008b; Blake & Fox, 1974; Moradi et al., 2005) and afterimages (Gilroy & Blake, 2005; Tsuchiya & Koch, 2005; van Boxtel et al., 2010) induced by interocularly suppressed stimuli.

Representations of eye gaze directions at a higher, object-centered level of visual processing, however, seem to require visual awareness. The absence of high-level, i.e., size-independent, eye gaze adaptation without awareness is consistent with recent studies that found high-level face adaptation aftereffects to be virtually eliminated by interocular suppression (Amihai et al., 2011; Moradi et al., 2005; Shin et al., 2009; Stein & Sterzer, 2011). These previous studies investigated aftereffects induced by *invariant* facial features, such as identity, age, or gender. By contrast, eye gaze, like facial expressions, is a *changeable* (i.e., dynamical) facial feature (Haxby et al., 2000). Our present results do not support a strict differentiation in the role of visual awareness in coding changeable vs. invariant facial features. Instead, the processing of certain aspects of emotionally charged stimuli, rather than changeable facial features in general, appears to escape strong suppression present at higher levels of the visual hierarchy (Adams et al., 2010; Anderson, Siegel, White, & Barrett, 2012; Jiang, Costello, Fang, Huang, & He, 2006; but see Yang et al., 2010), perhaps via a subcortical pathway that bypasses visual cortex, is less susceptible to interocular suppression, and responds to emotionally arousing stimuli (Jiang & He, 2006; Pasley et al., 2004; Williams et al., 2004).

Similarly, the advantage of faces with direct gaze in gaining access to awareness during CFS (Stein et al., 2011b) could reflect the arousal value of eye contact (Nichols & Champness, 1971) and may be mediated by subcortical structures such as the amygdala (George, Driver, & Dolan, 2001; Kawashima et al., 1999). Whereas such a coarse signal discriminating between different arousal values ("looking at me" vs. "not looking at me," e.g., Emery, 2000) may be independent of conscious awareness, object-centered high-level visual representations of specific eye gaze directions appear to require awareness.

The dissociation between intact adaptation to low-level components of eye gaze and abolished high-level eye gaze adaptation without awareness dovetails with

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current multilevel accounts of interocular suppression (Sterzer, Kleinschmidt, & Rees, 2009; Tong, Meng, & Blake, 2006). Such accounts posit a gradual increase in the depth of suppression from early levels of the visual system that represent simple visual features to higher levels of visual processing that represent more complex and abstract stimulus properties (Nguyen, Freeman, & Alais, 2003; Sheinberg & Logothetis, 1997).

In conclusion, our study demonstrates that only low-level aspects of eye gaze can be represented unconsciously under interocular suppression, whereas high-level eye gaze adaptation depends on visual awareness. These findings provide novel insights into the coding of eye gaze directions in the human visual system and expand our knowledge about the extent and limits of unconscious processing under interocular suppression.

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Appendix

Gaze angles of adapting and test stimuli

To relate the percentages of gaze deviation of the adapting and test stimuli to actual angles of gaze, we asked eight observers to compare the gaze directions of faces that were generated in FaceGen and used in the gaze adaptation experiments to the gaze directions of face photographs of a female young adult model. Photographs were taken while the model was keeping her head straight and was looking at reference markers corresponding to 0° left to 50° left (in steps of 5°). These photographs were then converted to grayscale and cropped to an oval shape that had the same size as the FaceGen stimuli from the adaptation experiments and excluded external facial features (see Figure A1). Participants compared the gaze direction of these 11 photographs to the gaze direction of an adapting stimulus looking maximally to the left (−100%, see Figure 1a) and to the gaze directions of a test stimulus displaying the four test deviations (to the left, i.e., −40%, −30%, −20%, and straight, i.e., 0% see Figure 1a). On each trial, 1 of the 11 photographs was paired with one FaceGen stimulus. One stimulus was centered directly above and the other directly below a central fixation point. Participants indicated whether the upper or the lower stimulus was gazing more to the left by pressing the corresponding arrow key. We asked participants to respond as accurately as possible and to take as much time as needed. There were 110 trials in which each combination of 11 gaze directions of the

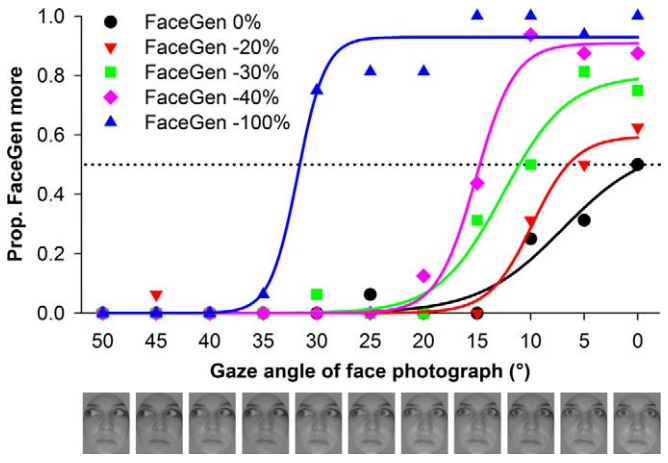

Figure A1. Results from the gaze judgment experiment. Shown is the mean proportion of trials in which participants judged the FaceGen stimulus to be looking more to the left than the face photograph, as a function of the gaze deviation of the FaceGen stimulus and the gaze angle of the face photograph. The data from each FaceGen gaze deviation are modeled with a sigmoidal function.

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face photograph, five gaze directions of the FaceGen stimuli, and two stimulus positions occurred once. Trial order was randomized. To determine the corresponding gaze angle for the gaze directions of the FaceGen stimuli, we averaged the proportion of trials in which observers judged the FaceGen stimuli to be looking more to the left than the face photograph, separately for all gaze directions of the FaceGen stimuli and the face photograph. For each FaceGen deviation we then fitted a sigmoidal function

$$y = \frac{a}{1 + e^{-\left(\frac{x - x_0}{b}\right)}} \quad (1)$$

to the data to estimate the respective point of subjective equality (PSE, i.e., the point at which participants judged the FaceGen stimulus to be looking more to the left in 50% of the trials). Fits were good (all $R^2 > 0.95$). For a FaceGen gaze deviation of −100% the PSE was at a gaze angle of 31.6° left, for −40% the PSE was 14.8° left, for −30% the PSE was 11.1° left, for −20% the PSE was 6.5° left, and for 0% the PSE was 0.9° right. These values are in good agreement with previous eye gaze adaptation studies that typically used adapting stimuli with a gaze angle of 25° and test stimuli with gaze angles of 10°, 5°, and 0° (Calder et al., 2008; Jenkins et al., 2006). In further support of this notion, the raw (unfitted) data showed that the FaceGen gaze deviations of −30%, −20%, and 0% were judged to be looking more to the left than the face photographs with gaze angles of 10°, 5°, and 0°, respectively, in exactly 50% of the trials (Figure A1).

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