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High-level face shape adaptation depends on visual awareness: Evidence from continuous flash suppression

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When incompatible images are presented to the two eyes, one image dominates awareness while the other is rendered invisible by interocular suppression. It has remained unclear whether complex visual information can reach high-level processing stages in the ventral visual pathway during such interocular suppression. Here, we asked whether basic face shape, which is thought to be encoded in areas of the ventral stream, can be processed without visual awareness. We measured aftereffects induced by prolonged exposure to distorted faces during continuous flash suppression. Despite constant physical stimulation, in some trials the adaptor face was fully suppressed from awareness, while in other trials it overcame suppression and became partially visible. Aftereffects were induced even by entirely invisible adaptors, albeit reduced compared to partially visible adaptors, and only when adaptor and test stimuli were presented in the same size to the same eye. However, when adaptor and test stimuli were presented to different eyes or to the same eye but in different sizes, aftereffects were restricted to partially visible adaptors. These results suggest that a monocular, low-level component of face shape adaptation escapes interocular suppression and can proceed without visual awareness. By contrast, high-level components of basic face shape encoding involving ventral stream processing are eliminated by interocular suppression and require visual awareness.

Keywords: adaptation, face processing, face shape, binocular rivalry, interocular suppression, visual awareness

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Introduction

When visual information is ambiguous or conflicting, perception can fluctuate between different interpretations of physically identical sensory input. Because of this intriguing dissociation between conscious visual perception and physical stimulus characteristics, such bi- or multistable visual phenomena provide a unique window into the neural correlates and behavioral consequences of unconscious and conscious visual processing (Kim & Blake, 2005; Leopold & Logothetis, 1999; Sterzer, Kleinschmidt, & Rees, 2009). One prominent example of bistable perception is binocular rivalry, which occurs when dissimilar images are presented to the two eyes at corresponding visual field locations. Rather than perceiving one composite percept, observers experience perceptual alternations between the two stimuli. Binocular rivalry has been exploited to pinpoint the neural and behavioral concomitants of visual awareness (Tong, Meng, & Blake, 2006) and to track the fate of unconscious information associated with the perceptually suppressed stimulus (Lin & He, 2009). A number of studies found that basic stimulus properties—such as orientation, spatial frequency, color, or translational motion—that are known to be processed in early visual cortical areas can be encoded without awareness (for a comprehensive review, see Lin & He, 2009). However, it has remained unclear to what extent more complex visual processing involving higher level visual areas is preserved during interocular suppression.

Converging evidence from human neuroimaging and behavioral priming studies has indicated that stimuli known to be strongly represented in areas along the dorsal stream, such as manipulable objects (Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2008; Fang & He, 2005) and numerical stimuli (Bahrami et al., 2010), continue to be processed when rendered invisible by interocular suppression. By contrast, it is less clear whether suppressed information reaches areas in the ventral visual pathway that mediate

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object and face recognition. A number of studies found neural activity in the ventral stream to be virtually eliminated during interocular suppression (Fang & He, 2005; Pasley, Mayes, & Schultz, 2004; Sheinberg & Logothetis, 1997; Tong, Nakayama, Vaughan, & Kanwisher, 1998).

However, more recent neuroimaging studies revealed weak responses to invisible images of faces in face-sensitive cortical areas (Jiang & He, 2006) and even showed that distributed patterns of brain activity in ventral stream areas contain information that distinguishes suppressed faces and houses (Sterzer, Haynes, & Rees, 2008). Similarly, electro- and magnetoencephalographic markers of face processing in ventral cortical areas differentiate between invisible faces and scrambled faces (Jiang et al., 2009) as well as between invisible faces and houses (Sterzer, Jalkanen, & Rees, 2009). It is currently unknown whether such weak residual traces of activity in the ventral stream manifest themselves in perception and behavior. Several behavioral studies failed to reveal evidence for preserved ventral stream processing during interocular suppression. For instance, it has repeatedly been shown that priming effects triggered by high-level stimuli that are processed in ventral cortical areas, such as words (Zimba & Blake, 1983), line drawings of objects (Cave, Blake, & McNamara, 1998), and images of vehicles and animals (Almeida et al., 2010, 2008), are eliminated during interocular suppression.

Another behavioral measure that is tightly coupled to neural coding can be derived from visual aftereffects induced by visual adaptation (Clifford & Rhodes, 2005; Frisby, 1979; Thompson & Burr, 2009). When adaptor stimuli are rendered invisible, visual aftereffects provide a means for gauging the boundaries of neural processing without awareness (Blake & He, 2005). In high-level vision, aftereffects resulting from prolonged viewing of face stimuli have been extensively studied to gain insight into the coding properties of different facial attributes, such as general face shape, identity, gender, race, and facial expression (e.g., Hsu & Young, 2004; Leopold, O'Toole, Vetter, & Blanz, 2001; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & MacLin, 1999). Typically, adaptation to a specific facial attribute biases subsequent perception of an ambiguous face away from the adapted attribute. For example, the so-called face identity aftereffect refers to the facilitated identification of a particular face exemplar after the prolonged exposure to its "anti-face" (Leopold et al., 2001).

If such face aftereffects could be induced by invisible faces, this would provide strong evidence for perceptually effective ventral stream processing despite interocular suppression. However, to date, there is little evidence for face adaptation without awareness. For example, Moradi, Koch, and Shimojo (2005) found the strength of the face identity aftereffect to depend on the visibility of the adaptor face. When the adaptor face was rendered subjectively invisible by interocular suppression, no face identity aftereffect was observed. Gender and expression aftereffects are reduced even by incomplete suppression (Adams, Gray, Garner, & Graf, 2010; Shin, Stolte, & Chong, 2009).[1] When complete unawareness of the adaptor face is ensured, gender, race, and expression aftereffects are totally extinguished (Amihai, Deouell, & Bentin, 2011; Yang, Hong, & Blake, 2010). This suggests that competition between rivaling images is resolved before the neural site underlying these face aftereffects.

However, the elimination of face aftereffects induced by such specific facial attributes does not necessarily imply that perceptually or behaviorally effective information about a suppressed visual object does not reach ventral cortical areas at all. For illustration, consider the face identity aftereffect. The coding of identity trajectories along a "face space" that forms the basis of the facial identity aftereffect presumably relies on the most anterior portions of the inferotemporal cortex (Furi, van Rijsbergen, Treves, & Dolan, 2007; Leopold, Bondar, & Giese, 2006; see also Kriegeskorte, Formisano, Sorger, & Goebel, 2007). Since depth of suppression during binocular rivalry is known to increase along the ventral stream (Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Nguyen, Freeman, & Alais, 2003), the absence of a face identity aftereffect leaves open the possibility that more basic object properties might still be processed during interocular suppression. In support of that notion, upright faces and familiar letters overcome interocular suppression more quickly than inverted faces and unfamiliar letters, respectively (e.g., Jiang, Costello, & He, 2007). This hints at the possibility that at least some stimulus properties known to be extracted in object-sensitive areas of the ventral stream remain effective during suppression.

In the present study, we sought to probe the coding of basic face shape without visual awareness. We examined the effect of interocular suppression on face shape, or figural face, aftereffects. Face shape aftereffects refer to the repeatedly reported phenomenon that prolonged exposure to a visible, systematically distorted face makes a subsequently viewed face appear distorted in the opposite direction (e.g., MacLin & Webster, 2001; O'Leary & McMahon, 1991; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Watson & Clifford, 2003; Webster & MacLin, 1999). Face shape aftereffects are generated, at least to some degree, by coding mechanisms specific to faces. For example, adaptation to an undistorted face has no effect on the perception of a subsequently presented distorted face (Webster & MacLin, 1999). This implies that undistorted, normal-looking faces have a special status and represent a neutral point or norm in face shape space. By contrast, in the case of the classical aftereffects induced by simple visual features, such as size, adaptation operates along a continuous dimension, without a neutral point (e.g., Köhler & Wallach, 1944). Furthermore, face shape aftereffects are reduced when the adaptor and the test face are displayed in opposite orientations (Watson & Clifford, 2003; Webster & MacLin, 1999), and

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opposite face shape aftereffects can be induced concurrently in upright and inverted faces (Rhodes et al., 2004). This orientation selectivity suggests that configural coding mechanisms characteristic for face-related tasks (Yin, 1969) are engaged by face shape adaptation.

Importantly, however, face shape aftereffects induced by adaptation to inverted faces are of equal strength as face shape aftereffects generated by upright faces, when tested with the corresponding face orientation (Rhodes et al., 2004; Robbins, McKone, & Edwards, 2007; Watson & Clifford, 2003; Webster & MacLin, 1999; Zhao & Chubb, 2001). In contrast, face identity aftereffects are more pronounced for upright than for inverted faces (Rhodes, Evangelista, & Jeffery, 2009). This difference in orientation sensitivity indicates that partly distinct neural mechanisms are involved in the face shape and the face identity aftereffect, respectively. In addition, crucial task differences distinguish the two adaptation paradigms. The face identity adaptation paradigm requires observers to discriminate individual faces, thereby engaging expert face processing mechanisms. By contrast, face shape aftereffects generalize across facial identities, again pointing to the involvement of a less abstract, more general shape coding mechanism. Whereas face identity aftereffects reflect adaptation of high-level, orientation-sensitive expert face coding mechanisms, face shape aftereffects rely rather on mid-level shape coding mechanisms that are less sensitive to face orientation (cf. Rhodes et al., 2009) and involve the adaptation of neurons coding general face shape (Jeffery, Rhodes, & Busey, 2006). In the light of these distinct characteristics, we considered it possible that face shape aftereffects would be less affected by interocular suppression than face identity aftereffects.

In the present study, we measured the effect of prolonged exposure to a contracted or expanded adaptor face on the perception of a subsequently presented face when the adaptor face was perceptually suppressed by continuous flash suppression (CFS; Tsuchiya & Koch, 2005). CFS is a variant of binocular rivalry in which dynamic, high-contrast Mondrian-like masks flashed to one eye suppress a stimulus presented to the other eye from awareness. Recently, CFS has been successfully applied to demonstrate low-level visual aftereffects induced by entirely invisible adaptors (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008a, 2008b; Kanai, Tsuchiya, & Verstraten, 2006; Maruya, Watanabe, & Watanabe, 2008). Furthermore, CFS was used in those few studies that uncovered residual neural responses to suppressed stimuli in ventral cortical areas (Jiang & He, 2006; Jiang et al., 2009; Sterzer et al., 2008; Sterzer, Jalkanen et al., 2009). If such residual responses contained perceptually effective face shape information, we would expect to observe face shape aftereffects induced by invisible adaptor stimuli. Alternatively, if preserved neural processing in ventral areas during suppression did not contain perceptually effective face shape information, aftereffects would depend on the visibility of the adaptor face.

Experiment 1

Methods

Participants

Twelve observers (four females, mean age = 25.4 years) with normal or corrected-to-normal vision participated in Experiment 1. All were naive to the purpose of the study.

Apparatus and stimuli

Participants viewed a pair of dichoptic displays on a Samsung 19-inch CRT monitor (1024 × 768 pixel resolution, 60-Hz frame rate) through a custom-built mirror stereoscope, with the subjects' heads stabilized by a chin-and-head rest at an effective viewing distance of 50 cm. To promote stable binocular alignment, the mirrors were adjusted for each observer. Visual stimuli were presented with Matlab (The MathWorks, Natick, MA), using the Cogent 2000 toolbox (www.vislab.ucl.ak.uk/cogent.php) on a Pentium 4 PC.

Stimuli were presented on a black screen. Two red frames (10.0° × 10.0°) were displayed side by side on the screen (horizontal center-to-center distance of 18.0°), such that one frame was presented to each eye. To support binocular alignment, fusion contours (width = 0.8°) consisting of randomly distributed black and white pixels were displayed within the red frames. The area within each frame was uniformly gray and a red fixation dot (0.7° × 0.7°) was drawn in the center of each frame. Observers were asked to maintain stable fixation throughout experimental blocks.

Face stimuli were generated using FaceGen Modeller 3.1 (Singular Inversions, www.facegen.com), a software package widely used in face perception research (e.g., Oosterhof & Todorov, 2008). We selected five facial identities (all male) to create adaptor stimuli and five different facial identities (all male) to create test stimuli. Faces were then converted to grayscale and cropped to an oval shape (6.6° × 8.0°) to remove external facial features. For the adaptor stimuli, each facial identity was distorted using the spherize function implemented in Adobe Photoshop (e.g., Jaquet & Rhodes, 2008; Rhodes, Jeffery, Clifford, & Leopold, 2007; Rhodes et al., 2003, 2004) to generate maximally contracted (−85%) and maximally expanded (+75%) faces (Figure 1a). For the test stimuli, each facial identity was distorted using the spherize function at the following levels: −20%, −10%, −5%, +5%, +10%, +20% (Figure 1b). Finally, all face stimuli were equalized for global contrast and luminance, and the edges of the ovals were blurred into the background using a Gaussian filter.

Procedure

Each trial started with a 1000-ms presentation of the red frames, the fusion contours, and the fixation dot only. Next, high-contrast colored Mondrian-like masks (8.4° × 8.4°;

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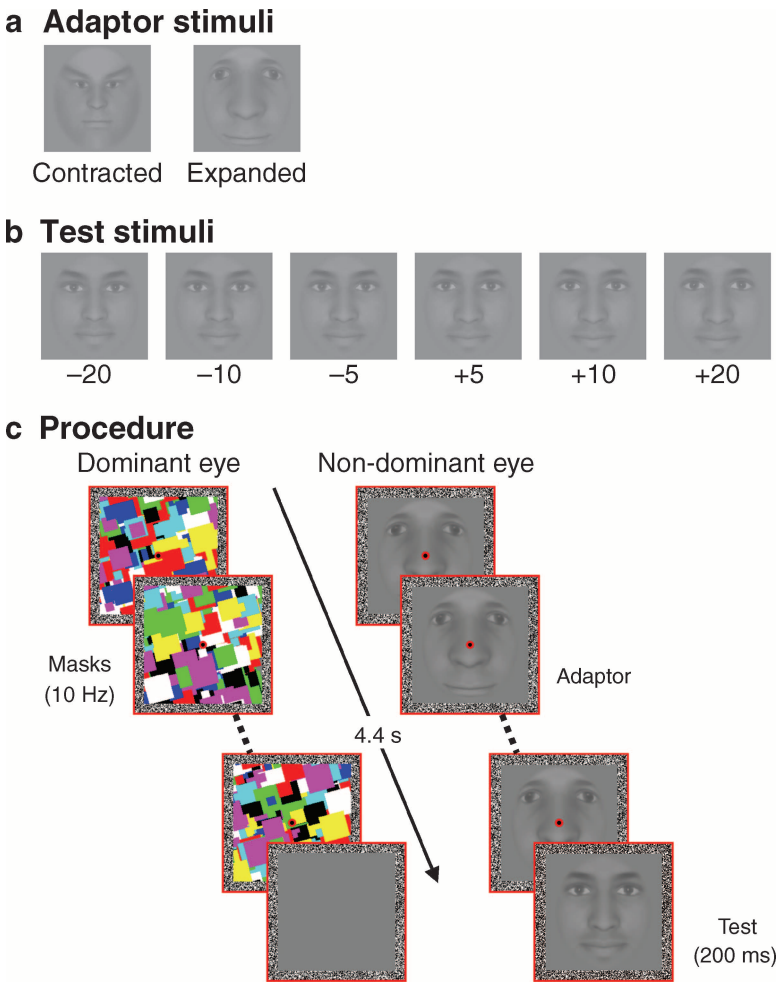

Figure 1. Sample stimuli and schematic of a sample trial. (a) Examples of contracted and expanded adaptor faces. (b) One test face at all six distortion levels from maximally contracted (−20) to maximally expanded (+20). (c) A schematic of a sample trial from Experiment 1 in which the adaptor and the test face had the same size and were shown to the same eye.

Stein, Senju, Peelen, & Sterzer, 2011) flashing at 10 Hz were presented to the participants' dominant eye while an adaptor stimulus was gradually introduced to the non-dominant eye (ocular dominance was determined prior to the experiment by the Miles (1930) test). The contrast of the adaptor stimulus was ramped up linearly from 0% to 100% within a period of 400 ms from the beginning of the trial (to avoid abrupt transients) and then remained constant for another 4000 ms (Figure 1c). During this adapting period, observers were required to press the key "1" with their left hand as soon as any part of the adaptor face became subjectively visible. We did not require subjects to hold down the key for the total time the adaptor was perceptually dominant, since initial piloting had indicated that in most trials in which the adaptor overcame CFS, the whole face or parts of the face remained at least partially visible until the end of the adapting period (also documented by Amihai et al., 2011). Participants were instructed to adopt a very liberal response criterion and to press "1" even when having "only a vague idea of seeing a part or parts of a face."

Immediately after the adapting period, the fixation dot and the masks disappeared and a test face was presented for 200 ms to the participants' non-dominant eye, followed by the 1500-ms presentation of a blank screen, containing the red frames and the fusion contours only. Participants pressed the left or the right arrow key with their right hand to indicate whether the test face appeared to be rather contracted or expanded. Observers were informed that response times would not be recorded and were instructed to be as accurate as possible. At the end of the trial, a small question mark (0.7° × 0.7°) was displayed for 1700 ms to once again offer participants the chance to press the key "1" if they had actually seen parts of the adaptor face but had failed to report that during the adapting period.

Each block consisted of 72 trials in which each combination of two adaptation conditions (contracted, expanded) and six test face distortion levels appeared equally often. The identities of the adaptor and test faces were randomized. Nine subjects completed six blocks, two subjects completed seven blocks, and one participant completed nine blocks. Before the testing session started, participants

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were shown examples of contracted and expanded face stimuli similar to the adaptor and test stimuli. These sample stimuli were not used in the actual experiment. Subsequently, observers received one familiarization block consisting of 72 trials. During this block, subjects judged the distortion of the test faces used in the main experiment, without a preceding adapting period.

Finally, subsequent to the main experiment, seven of the twelve observers participated in an additional control experiment in which we tested whether participants could discriminate the distortion direction of subjectively invisible adaptor faces. This control experiment consisted of two blocks containing 72 trials each that were identical to the trials in the main experiment, except that participants now discriminated the distortion of the adaptor faces. Furthermore, to avoid response conflict in trials in which the adaptor and the test face had different distortion directions and to prevent subjects from inferring the adaptor face distortion from the potentially perceivable aftereffect, the distorted test faces were replaced by scrambled versions. Five scrambled faces were created by dividing the inner oval of each original test face in 112 squares and randomly recomposing them. Subsequently, they were assigned the same global contrast and luminance as the test faces.

Results and discussion

Trials were classified according to participants' subjective awareness as *partial suppression* (i.e., the adaptor face became visible at some point during the adapting period) or *full suppression* (i.e., the adaptor was invisible during the whole adapting period) trials. The data from one subject could only be included in the analysis of full suppression trials, due to an insufficient number of partial suppression trials (2.8% of all trials). For the remaining subjects, the mean percentage of full suppression trials was 50.4% (*SD* = 15.6%). We first analyzed responses separately for partial suppression and full suppression trials. The proportions of expanded responses were submitted to repeated measures ANOVAs with the within-subjects factors adaptation (contracted, expanded) and test distortion (six levels).

Most importantly, aftereffects were induced both by partially visible as well as by fully invisible distorted faces,

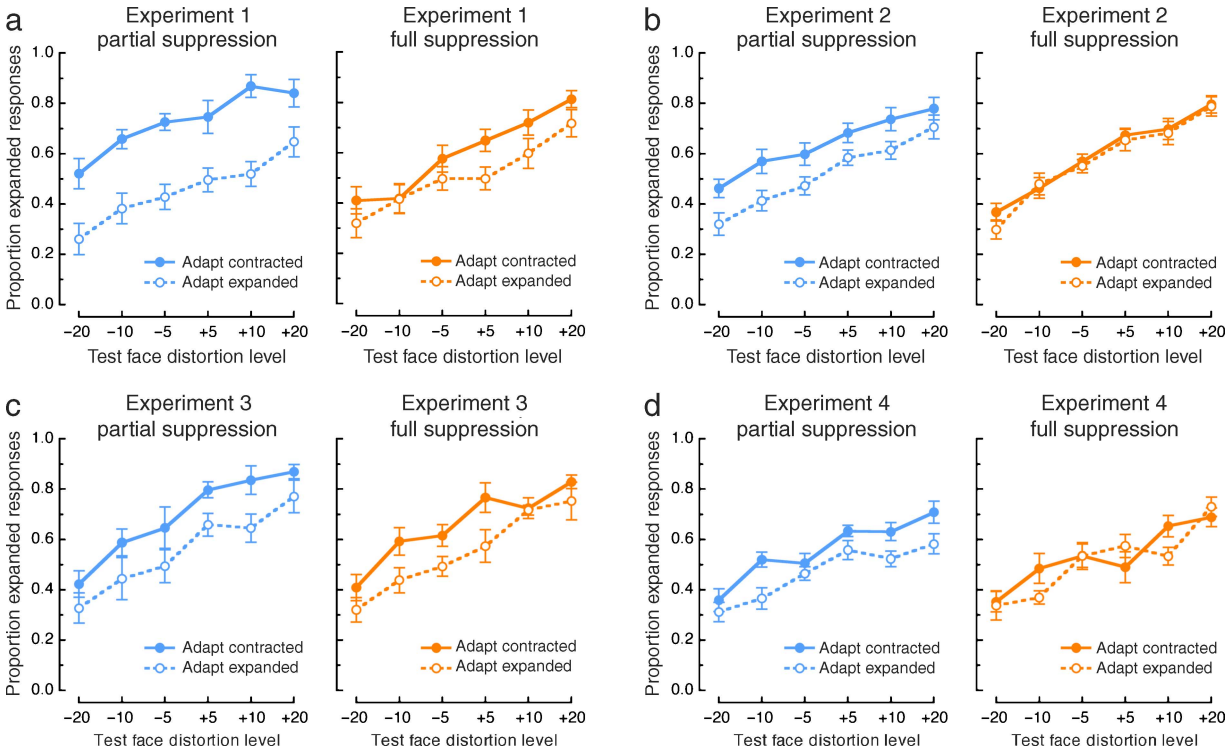

Figure 2. Results from the adaptation experiments. Mean proportion of expanded responses as a function of adaptation condition and test face distortion level, separately for Experiments 1–4 (a–d) and according to subjective perceptual suppression of the adaptor face (full suppression vs. partial suppression), are shown. Negative test face distortion levels refer to contracted test faces, while positive test face distortion levels refer to expanded faces. In Experiments 1–3, adaptor and test faces had the same size; in Experiment 4, we introduced a twofold size change between adaptor and test. In Experiments 1, 3, and 4, adaptor and test faces were presented to the same eye; in Experiment 2, they were shown to different eyes. During partial suppression, face shape aftereffects were found across all experiments. During full suppression, residual aftereffects were observed only when the adaptor face was presented at the same size and to the same eye as the test face (Experiments 1 and 3). Error bars denote standard errors of the means.

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as demonstrated by significant main effects of adaptation both for partial suppression, $F(1, 10) = 50.99$, $p < 0.001$, and for full suppression, $F(1, 11) = 6.63$, $p = 0.026$. As expected, there were significant main effects of test distortion, both for partial suppression, $F(5, 50) = 16.85$, $p < 0.001$, as well as for full suppression, $F(5, 55) = 18.23$, $p < 0.001$, showing that the overall proportion of expanded responses increased for relatively more expanded test faces. Finally, there was no significant interaction between adaptation and test distortion, neither for partial suppression, $F(5, 50) < 1$, nor for full suppression, $F(5, 55) = 1.93$, $p = 0.104$.

As evident from Figure 2a, the difference between the adaptation conditions, i.e., the strength of the face shape aftereffect, was larger for the partial suppression trials than for the full suppression trials. This impression was supported by a significant interaction between adaptor visibility (partial suppression, full suppression) and adaptation (contracted, expanded), $F(1, 10) = 13.41$, $p = 0.004$. Thus, awareness of the adaptor face boosted face shape aftereffects. Nevertheless, face shape adaptation was still observed even for subjectively invisible adaptors.

The results from the control experiment demonstrated that when participants did not report subjective visibility of the adaptor, they were also unable to discriminate the adaptor's distortion direction. In full suppression trials, mean accuracy in discriminating the distortion direction of the adaptor face was 49.3% (not significantly different from chance, $t(6) < 1$). In partial suppression trials, i.e., when participants reported subjective visibility of the adaptor, participants' accuracy in discriminating the distortion direction of the adaptor face was near ceiling (averaged across six observers, 95.5% correct; see Figure 3; one participant experienced only full suppression trials in the control experiment).

At first glance, the results from Experiment 1 seem to suggest that interocular suppression does not eliminate face shape aftereffects. However, the fact that both the adaptor and the test face were presented to the same eye imposes an important caveat to the interpretation of Experiment 1. It is possible that eye-specific mechanisms, presumably residing in lower levels of the visual hierarchy, contributed to the generation of aftereffects. To exclude this possibility, previous studies investigating the effect of interocular suppression on face adaptation displayed adaptor and test stimuli to different eyes (Adams et al., 2010; Amihai et al., 2011; Shin et al., 2009; Yang et al., 2010).

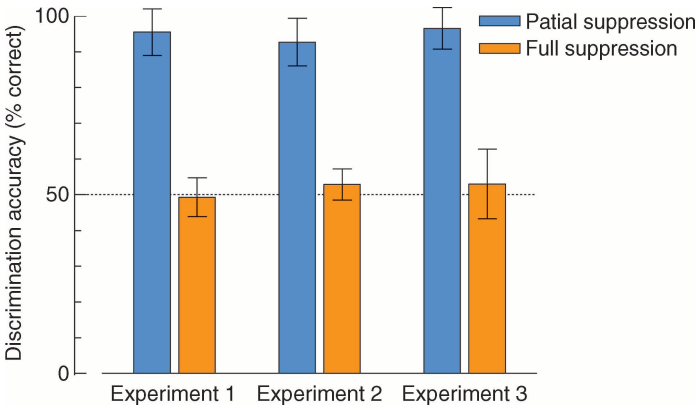

Figure 3. Results from the control experiments. Bar plots depict mean accuracy in discriminating the distortion of the adaptor face, depending on subjective perceptual suppression of the adaptor face. Error bars denote 95% confidence intervals for the respective comparison against chance performance (dotted line).

Experiment 2

In Experiment 2, we investigated the degree of interocular transfer of face shape aftereffects caused by visible and invisible adaptors. In visual adaptation paradigms, interocular transfer reflects the involvement of binocular neurons (e.g., Blake, Overton, & Lema-Stern, 1981), pointing to (but not necessarily implying) a cortical origin of the observed aftereffect (e.g., Blakemore & Campbell, 1969; Maffei, Fiorentini, & Bisti, 1973). Clearly, the face shape aftereffect induced by visible adaptors is not solely the result of low-level adaptation, since it survives a threefold size change between the adaptor and the test face (Jaquet & Rhodes, 2008; Jeffery et al., 2006; Rhodes et al., 2007; Yamashita, Hardy, De Valois, & Webster, 2005; Zhao & Chubb, 2001). Nevertheless, it is possible that lower level adaptation plays a role in the generation of the face shape aftereffect. For example, although not eliminated, the face shape aftereffect is reduced when adaptor and test faces have different sizes (Jeffery et al., 2006; Yamashita et al., 2005; Zhao & Chubb, 2001) or when they are viewed from different viewpoints (Jeffery et al., 2006; Jeffery, Rhodes, & Busey, 2007). To our knowledge, no previous study examined the interocular transfer of the face shape aftereffect. If adaptation did not fully transfer to the nonadapted eye, this would indicate a distinct contribution of neurons with an ocular preference to the face shape aftereffect. The crucial question was whether face shape aftereffects induced by invisible adaptor faces in Experiment 1 could have been caused by the adaptation of such neurons only. If true, in Experiment 2 we would expect to observe no face shape aftereffect from invisible adaptors.

Methods

Participants

A new group of 20 observers (seventeen females, mean age = 23.5 years) with normal or corrected-to-normal vision participated in Experiment 2. All were naive to the purpose of the study.

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Apparatus, stimuli, and procedure

Experiment 2 was the same as Experiment 1, except for the following changes. The test face was now presented to the same eye as the preceding CFS masks. Piloting work showed that this resulted in stronger forward masking by the high-contrast CFS masks than in Experiment 1 (see Turvey, 1973). To attenuate the effect of such monoptic forward masking on test face visibility, a blank screen displayed for 117 ms was inserted between the offset of the adaptor face and the onset of the test face. The same changes were applied to the control experiment. In Experiment 2, eleven subjects completed six blocks and nine subjects completed seven blocks of the main experiment. Nineteen out of the 20 participants were also tested in the control experiment.

Results and discussion

The data from two subjects could only be included in the analysis of full suppression trials, due to an insufficient number of partial suppression trials (0.2% and 1.4% of all trials, respectively). For the remaining subjects, the mean percentage of full suppression trials was 51.2% (SD = 13.7%).

For the partial suppression trials, there was a significant main effect of test distortion, $F(5, 85) = 29.10$, $p < 0.001$, and a significant main effect of adaptation, $F(1, 17) = 17.63$, $p = 0.001$. The interaction between these two factors was not significant, $F(5, 85) < 1$. Hence, adaptation to partially visible faces induced an interocular face shape aftereffect. By contrast, for the full suppression trials there was only a significant main effect of test distortion, $F(5, 95) = 43.51$, $p < 0.001$, but no significant main effect of adaptation, $F(1, 19) = 1.50$, $p = 0.235$, and no significant interaction, $F(5, 95) < 1$. Thus, face shape aftereffects were restricted to trials in which adaptor faces overcame suppression and were eliminated when the adaptor was subjectively invisible (see Figure 2b). This conclusion was also supported by a significant interaction between adaptor visibility and adaptation, $F(1, 17) = 10.53$, $p = 0.005$.

Mean accuracy in discriminating the distortion direction of the adaptor face was 52.9% in full suppression trials (not significantly different from chance, $t(16) = 1.38$, $p = 0.186$) and 92.7% in partial suppression trials (Figure 3).

In sum, the results from Experiment 2 indicate that there is no interocular transfer of adaptation to invisible face shape. Furthermore, the direct comparison between Experiments 1 and 2 showed that for partially visible adaptors interocular transfer reduced the size of the aftereffect, as demonstrated by a significant interaction between experiment (Experiment 1 vs. 2) and adaptation, $F(1, 27) = 10.34$, $p = 0.003$. This points to the involvement of neurons with an ocular preference in the generation of the full-blown face-shape aftereffect. However, before drawing firm conclusions from the comparison of Experiments 1 and 2 (see General discussion section), we first have to rule out that the small temporal gap between adaptation and test that was newly introduced in Experiment 2 caused the reduced aftereffect.

Experiment 3

In Experiment 3, we wished to exclude the possibility that this temporal gap could explain the absence of face shape aftereffects during full suppression observed in Experiment 2. Thus, in Experiment 3, we sought to replicate the eye-specific aftereffects induced by invisible adaptor faces revealed in Experiment 1 but introduced the same temporal gap as in Experiment 2. Furthermore, we now tested all participants in the control experiment to assess the objective invisibility of the distortion direction of the adaptor face in individual observers.

Methods

Participants

Six subjects (four females, mean age = 23.8 years) participated in Experiment 3. Of them, three had participated in Experiment 1 before, and three had participated in Experiment 2 before. These individuals were selected solely according to their availability at the time of Experiment 3.

Apparatus, stimuli, and procedure

Experiment 3 was the same as Experiment 1, but as in Experiment 1 we inserted a blank screen displayed for 117 ms between the offset of the adaptor face and the onset of the test face. In Experiment 3, four subjects completed six blocks, one subject completed seven blocks, and one subject completed eight blocks of the main experiment. All six participants were also tested in the control experiment.

Results and discussion

The mean percentage of full suppression trials was 51.2% (SD = 14.3%).

For the partial suppression trials, there was a significant main effect of test distortion, $F(5, 25) = 16.55$, $p < 0.001$, and a significant main effect of adaptation, $F(1, 5) = 74.03$, $p < 0.001$. The interaction between adaptation and test distortion was not significant, $F(5, 25) < 1$. Importantly, for the full suppression trials, there were again significant main effects of test distortion, $F(5, 25) = 16.40$, $p < 0.001$, and adaptation, $F(1, 5) = 22.84$, $p = 0.005$, but no significant interaction between the two, $F(5, 25) = 1.22$, $p = 0.327$ (see Figure 2c). In contrast to the previous experiments, aftereffects were not significantly amplified

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by adaptor visibility, as indicated by a non-significant interaction between adaptor visibility and adaptation, $F(1, 5) = 2.27$, $p = 0.192$. This might be attributable to the smaller sample size in Experiment 3.

Mean accuracy in discriminating the distortion direction of the adaptor face was 53.0% in full suppression trials (not significantly different from chance, $t(5) < 1$) and 96.6% in partial suppression trials (Figure 3). The interpretation of Experiment 3 critically depended on the adaptor face distortion being truly invisible in full suppression trials for all single observers. Single-sample z-tests (Adams et al., 2010; Almeida et al., 2008) showed that one observer's discrimination accuracy (63.9% correct) significantly exceeded chance performance ($p = 0.006$). Importantly, when this subject was excluded from the analysis of the full suppression trials, there was still a significant main effect of adaptation for the full suppression trials, $F(1, 4) = 18.05$, $p = 0.013$.

Thus, as in Experiment 1, a robust face shape aftereffect was induced by invisible adaptors displayed to the same eye as the test stimulus. These results show that interocular transfer and not the temporal gap between adaptor and test was the critical factor underlying the absence of the face shape aftereffect in Experiment 2. Taken together, the results from Experiments 1–3 suggest that without awareness only monocular, low-level components of face shape can be adapted.

Experiment 4

In Experiment 4, we sought to rule out two alternative explanations for our findings. First, because we presented adaptor and test faces in identical sizes, it could be argued that even the aftereffects induced by partially visible adaptors were caused by low-level adaptation rather than face-shape-specific high-level adaptation. In other words, our experimental protocol could have failed to induce high-level face shape adaptation. Alternatively, as some neurons in higher areas in the ventral visual pathway respond differentially to input from both eyes (Uka, Tanaka, Yoshiyama, Kato, & Fujita, 2000), it remains possible (albeit unlikely) that high-level face shape adaptation occurred even for invisible adaptor faces but, due to its potential ocular specificity, could not be measured when adaptor and test faces were presented to different eyes. We addressed these possibilities by introducing a twofold size change between the adaptor and test faces (Jeffery et al., 2006, 2007; Rhodes et al., 2007, 2004; Yamashita et al., 2005; Zhao & Chubb, 2001) but presented them to the same eye. If only low-level, retinotopic mechanisms were being adapted during partial suppression, in Experiment 4 no aftereffects would be expected even for partially visible adaptor faces. Alternatively, if higher level coding mechanisms with an ocular bias could be adapted without awareness, aftereffects should be observed during full suppression. By contrast, on the basis of the previous experiments, we conjectured that only low-level, monocular components of face shape can be encoded when rendered invisible by CFS and, thus, expected to observe no aftereffects from invisible faces.

Methods

Participants

A new set of 14 participants (two males, mean age = 24.6 years) took part in Experiment 4.

Apparatus, stimuli, and procedure

Experiment 4 was identical to Experiment 3, except for the sizes of the stimuli. The size of the adaptor faces was increased to 8.3° × 10.0°, while the size of the test faces was decreased to 4.1° × 5.0°. To accommodate the enlarged adaptor faces, the size of the red frames in which the face stimuli were presented was increased to 11.6° × 11.6°, and the CFS masks were enlarged accordingly (10.0° × 10.0°). Five subjects completed seven blocks and nine subjects completed six blocks. As we expected to observe no aftereffects from subjectively invisible adaptor faces, in Experiment 4 we did not include an additional control experiment.

Results and discussion

The data from two subjects could only be included in the analysis of partial suppression trials, due to an insufficient number of full suppression trials (5.3% and 10.3% of all trials, respectively). For the remaining subjects, the mean percentage of full suppression trials was 42.5% ($SD = 13.9\%$).

The analysis of the partial suppression trials yielded a significant main effect of test distortion, $F(5, 65) = 23.47$, $p < 0.001$, and a significant main effect of adaptation, $F(1, 13) = 10.12$, $p = 0.007$. The interaction was not significant, $F(5, 65) = 2.08$, $p = 0.079$. Thus, despite the size change between adaptor and test faces partially visible adaptors induced a face shape aftereffect (see Figure 2d). Replicating previous studies using fully visible faces (Jeffery et al., 2006; Yamashita et al., 2005; Zhao & Chubb, 2001), this aftereffect was of smaller magnitude than the aftereffects from adaptors of the same size as the test faces obtained in Experiments 1 and 3 (a mixed ANOVA with the between-subjects factor face size (same, different) and adaptation yielded a significant size-by-adaptation interaction, $F(1, 29) = 9.93$, $p = 0.004$, compare the subplots in Figure 2). Excluding the two subjects with an insufficient number of full suppression trials did not change the overall pattern of results (main effect of test distortion, $F(5, 55) = 30.43$, $p < 0.001$; main effect of adaptation, $F(1, 11) = 9.08$, $p = 0.012$; interaction,

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$F(5, 55) = 2.52$, $p = 0.040$). Hence, for partially visible adaptors our experimental protocol successfully induced face shape aftereffects that are unlikely to be accounted for by low-level, retinotopic coding mechanisms (Jeffery et al., 2006, 2007; Rhodes et al., 2007, 2004; Yamashita et al., 2005; Zhao & Chubb, 2001).

By contrast, for the full suppression trials, there was a significant main effect of test distortion only, $F(5, 55) = 15.77$, $p < 0.001$, but no significant main effect of adaptation, $F(1, 11) < 1$ (and no significant interaction, $F(5, 55) = 2.02$, $p = 0.091$), meaning that aftereffects were abolished when the adaptor remained subjectively invisible (see Figure 2b; the interaction between adaptor visibility and adaptation approached significance, $F(1, 11) = 4.48$, $p = 0.058$). As we presented adaptor and test faces to the same eye, these results render the possibility highly unlikely that the absence of interocular transfer without awareness (Experiment 2) could be ascribed to a crucial role of neurons with an ocular bias residing in higher levels of the visual hierarchy (Uka et al., 2000). Instead, the outcome of Experiment 4 further supports the idea that high-level face shape adaptation involving processing stages beyond low-level eye-specific coding mechanisms depends on visual awareness.

General discussion

In the present study, we set out to test whether basic face shape can be encoded without visual awareness. To that end, we measured the well-established face shape aftereffect and used CFS to suppress the adaptor face from visual awareness. Despite stimulation being constant, this resulted in trials in which the adaptor face was subjectively invisible and in trials in which the adaptor overcame suppression and was consciously perceived. This dissociation between physical stimulus information and conscious perception allowed us to gauge the effect of visual awareness on face shape adaptation. Subjective visibility of the adaptor face strongly influenced the strength of the face shape aftereffect (Experiment 1). When the potential contribution of low-level, purely monocular (Experiment 2) or retinotopic (Experiment 4) mechanisms was ruled out, we found no evidence for an aftereffect following the presentation of invisible adaptor faces. However, with the same physical stimulation, we observed significant face shape aftereffects when the adaptor face overcame suppression and became subjectively visible. This pattern of results suggests that visual awareness is necessary for processing basic face shape information.

In addition, the comparison of aftereffects induced by presenting the adaptor and the test face to the same eye (Experiments 1 and 3) or to different eyes (Experiment 2) indicated the contribution of eye-specific mechanisms to the generation of the full-blown face-shape aftereffect. Even for partially visible adaptors, we found only incomplete interocular transfer of face shape adaptation. Traditionally, such ocular specificity would have been interpreted as indicating that the involvement of peripheral sites situated between the retina and primary visual cortex amplified the observed behavioral aftereffect (e.g., Anstis & Moulden, 1970), as the proportion of monocularly driven neurons sharply declines in higher level visual areas downstream from primary visual cortex (e.g., Zeki, 1978). However, to be precise, it suffices to posit the participation of neurons with an ocular preference in mediating the aftereffect to account for incomplete interocular transfer. As some (weak) ocular preference has been observed even in higher visual areas of the ventral stream (Uka et al., 2000), caution is needed in linking eye-specific effects to specific anatomical structures. Furthermore, incomplete interocular transfer could also be explained by assuming that binocular neurons were actually adapted but lacked responsiveness during presentation of the test face (cf. Blake et al., 1981).

Consistent with the idea that the mechanisms mediating eye-specific adaptation to invisible faces are situated in lower levels of the visual hierarchy, we found no evidence for face shape aftereffects from invisible faces when the adaptor and the test face were shown to the same eye but in different sizes (Experiment 4). By contrast, aftereffects from partially visible adaptor faces persisted despite the size change between the adaptor and the test face, albeit at reduced strength compared to aftereffects induced by adaptors of the same size as the test stimuli. Previous studies found face aftereffects to be enhanced when the adaptor and test stimuli were presented at the same retinal position (Kovács, Zimmer, Harza, Antal, & Vidnyánszky, 2005; Kovács, Zimmer, Harza, & Vidnyánszky, 2007) and have implicated different visual cortical areas in mediating position-specific and position-invariant face aftereffects (Kovács, Cziraki, Vidnyánszky, Schweinberger, & Greenlee, 2008). Similarly, contrast polarity, spatial frequency, size, orientation, and viewpoint changes between the adaptor and test stimuli all reduce but not eliminate the size of face shape aftereffects (Jeffery et al., 2006, 2007; Yamashita et al., 2005; Zhao & Chubb, 2001). In conjunction with the present findings, this suggests that the face shape aftereffect does not exclusively index high-level face-selective processing but reflects adaptation at multiple levels of the visual system, presumably including neurons with an ocular preference and possibly even early, purely monocular neurons.

Importantly, our findings tentatively suggest that only this class of neurons adapts to distorted faces rendered invisible by interocular suppression. Such low-level adaptation without awareness is consistent with a number of studies that found early visual processing to be little impaired by conventional binocular rivalry (reviewed by Lin & He, 2009) or by other interocular suppression techniques such as CFS (Bahrami et al., 2008a, 2008b; Blake, Tadin, Sobel, Raissian, & Chong, 2006; Gilroy & Blake, 2005; Kanai et al., 2006; Maruya et al., 2008;

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Moradi et al., 2005; Tsuchiya & Koch, 2005; van Boxtel, Tsuchiya, & Koch, 2010). Earlier studies that examined the effect of interocular transfer on aftereffects induced by adaptors presented during interocular suppression found the tilt (Wade & Wenderoth, 1978), threshold elevation (Blake & Overton, 1979), and motion aftereffects (O'Shea & Crassini, 1981) to transfer interocularly, despite binocular rivalry during the adaptation period. However, the suppression technique used in these studies did not ensure subjective invisibility of the adaptor and is, therefore, more comparable to the present partial suppression condition in which we also found interocular transfer of the face shape aftereffect (Experiment 2).

To the best of our knowledge, only one previous study has explicitly assessed the degree of interocular transfer of aftereffects induced by fully invisible adaptors. Maruya et al. (2008) examined the effect of CFS on the motion aftereffect evoked by dynamical test patterns, which is assumed to reflect higher level motion processing. Their results bear a close resemblance to the outcome of the present study. Maruya et al. found the motion aftereffect to persist despite suppression but only if the invisible adaptor and the test pattern were presented to the same eye. When the adaptor and the test pattern were shown to different eyes, the motion aftereffect was restricted to visible adaptors. This was interpreted as demonstrating that only eye-specific low-level components of motion adaptation can proceed without awareness.

In line with this interpretation, the present findings suggest that only eye-specific low-level components of face shape adaptation resist interocular suppression. By contrast, binocular higher level components of face shape adaptation involving neurons beyond primary visual cortex appear to be entirely eliminated during suppression. Thus, visual awareness is necessary not only for adaptation to face identity, gender, race, and expression (Amihai et al., 2011; Moradi et al., 2005; Yang et al., 2010) but also for adaptation to basic face shape. The elimination of face shape adaptation by interocular suppression is consistent with a multilevel view of binocular rivalry in which suppression occurs at multiple levels of the visual system (Sterzer, Kleinschmidt et al., 2009; Tong et al., 2006) but deepens as one moves up the visual hierarchy (Nguyen et al., 2003), until near complete suppression in object-responsive areas of the ventral visual pathway (Fang & He, 2005; Moradi et al., 2005; Pasley et al., 2004; Sheinberg & Logothetis, 1997; Tong et al., 1998). This view leaves open the possibility that recently discovered neural markers of residual processing in ventral areas during interocular suppression might carry behaviorally effective information about other stimulus properties, such as category membership (Sterzer et al., 2008; Sterzer, Jalkanen et al., 2009), familiarity (Jiang et al., 2007), arousal and valence (Jiang, Costello, Fang, Huang, & He, 2006; Jiang & He, 2006; Jiang et al., 2009; Sterzer, Hilgenfeldt, Freudenberg, Bermpohl, & Adli, 2011; Yang, Zald, & Blake, 2007), or social relevance (Stein et al., 2011). Further studies are needed to elucidate the functional significance of such residual neural responses.

Before concluding, some limitations of the present study should be considered. First, face shape adaptation certainly does not capture all facets of high-level shape processing in the human visual system. Our findings, therefore, do not necessarily generalize to other aspects of high-level shape encoding. Nevertheless, face shape aftereffects have proven a particularly valuable tool for uncovering universal coding principles in high-level vision (e.g., Clifford & Rhodes, 2005). However, it is important to note that while visual aftereffects are tightly linked to underlying neural coding properties, they can, by their very nature, provide a measure of a change in subjective *perception* only. Therefore, it remains possible that residual information about the shape of interocularly suppressed stimuli feeds into systems supporting other processes than subjective perception, for example, attention or motor control. For that reason, studies applying other measures such as attentional orienting, response priming, electrophysiology, or neuroimaging will be needed to get a complete picture of the boundaries of high-level shape processing during interocular suppression.

Finally, our findings do not categorically rule out the possibility that face shape might still be processed when rendered invisible by means other than interocular suppression, such as masking, crowding, or inattention. For example, one potential drawback of using CFS to investigate the effect of awareness on the processing of face shape consists in the necessity to flash high-contrast masks consisting of various oriented lines and edges to one eye. Recently, Dickinson, Almeida, Bell, and Badcock (2010) demonstrated that face aftereffects can at least partially be accounted for by modeling the application of multiple local tilt aftereffects across the visual field. As tilt aftereffects can occur after very brief exposure (Dickinson, Han, Bell, & Badcock, 2010; Sekuler & Littlejohn, 1974), adaptation to oriented elements in (visible) CFS masks could have counteracted adaptation to the shape of (invisible) faces. However, at present only interocular suppression techniques such as CFS can be used for studying high-level aftereffects, since they constitute the only currently available method allowing for extended periods of reliable invisibility of complex stimuli such as face photographs.

In conclusion, we found high-level face shape aftereffects to be dependent on visual awareness of the adaptor face. Furthermore, the partial interocular transfer of face shape aftereffects tentatively points to the contribution of an eye-specific, possibly purely monocular system to the buildup of full-strength face-shape adaptation. Only this eye-specific low-level system appears to be adaptable during complete interocular suppression. In terms of "psychoanatomy" (Julesz, 1971; see also Blake, 1995), these findings suggest that the site of interocular suppression is situated between the sites mediating the eye-specific and binocular components of face shape adaptation. Thus,

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while the earliest stages of basic face shape encoding can proceed without awareness, face shape processing in higher level areas of the ventral stream requires visual awareness.

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Footnote

[1]See Yang et al. (2010) for a critical discussion of the evidence for facial expression adaptation without awareness reported by Adams et al. (2010).

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