Face adaptation depends on seeing the face

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Summary

Retinal input that is suppressed from visual awareness can nevertheless produce measurable aftereffects, revealing neural processes that do not directly result in a conscious percept. We here report that the face identity-specific aftereffect requires a visible face; it is effectively cancelled by binocular suppression or by inattentional blindness of the inducing face. Conversely, the same suppression does not interfere with the orientation-specific aftereffect. Thus, the competition between incompatible or interfering visual inputs to reach awareness is resolved before those aspects of information that are exploited in face identification are processed. We also found that the face aftereffect remained intact when the visual distracters in the inattention experiment were replaced with auditory distracters. Thus, cross-modal or cognitive interference that does not affect the visibility of the face does not interfere with the face aftereffect. We conclude that adaptation to face identity depends on seeing the face.

Introduction

Psychologists have perfected a number of techniques that render retinal inputs invisible yet that still result in visible aftereffects and other measurable phenomena, including orientation-specific adaptation (Blake and Fox, 1974; He et al., 1996; He and MacLeod, 2001; Montaser-Kouhsari et al., 2004; Rajimehr, 2004), motion aftereffect (Lehmkuhle and Fox, 1975; O'Shea and Crassini, 1981), and orientation contingent color aftereffect(White et al., 1978). This reveals the existence of stages in the visual processing hierarchy that precede regions that are necessary and sufficient for visual awareness; an inference Bela Julesz called *psycho-anatomy* (Julesz, 1971). The fact that some low-level aftereffects do not require awareness of the inducing stimulus raises the general question to what extent more complex aftereffects such as those for object identity that are mediated by neurons in the upper echelons of the ventral pathway, require visual awareness. Imaging (Moutoussis and Zeki, 2002; Pasley et al., 2004; Williams et al., 2004) and priming (Paller et al., 2003) experiments suggest that selected aspects of face processing can occur without conscious perception of the face. We therefore set out to test the dependency of the recently discovered face aftereffect on conscious perception (i.e., subjective visibility) of the inducing face.
The retinal input can be rendered perceptually invisible by presenting an incompatible image to the other eye. Binocular rivalry occurs when the visual system fails to establish correspondence between the two images. Each image then undergoes exclusive periods of visibility (dominance) and invisibility (suppression). Yet this perceptual suppression has little effect on the build-up of orientation-selective adaptation (Blake and Fox, 1974) and the linear-motion aftereffect (Lehmkuhle and Fox, 1975). How does binocular suppression affect face adaptation? In the first set of experiments we study adaptation to realistic face images (Leopold et al., 2001) under dichoptic viewing condition (that is, the two eyes receive different inputs). Identification of a specific face is selectively facilitated after a few seconds of adaptation to a face that has opposite global features (corresponding “anti-face”), whereas adaptation to an unrelated face slightly impairs identification (Leopold et al., 2001). If suppressed input reaches face selective neurons, then adaptation to such input might affect identification of subsequent faces. For comparison, we investigate the orientation-dependent aftereffect using the same setup.

Selective attention and task-relevance also affect conscious registration of visual inputs (Mack and Rock, 1998; Simons and Chabris, 1999). Attention is suggested to be involved in binocular suppression and other disappearance phenomena (Bonneh et al., 2001; Mitchell et al., 2004; Ooi and He, 1999). Whether inattention and binocular suppression influence the formation of aftereffects in the same manner is not known; for example, inattention (Chaudhuri, 1990) — but not binocular suppression (Lehmkuhle and Fox, 1975) — reduces the magnitude of the linear motion aftereffect. In contrast, binocular suppression (Wiesenfelder and Blake, 1990) — but not lack of attention (Aghdaee, 2004) — eliminates the spiral motion aftereffect. Thus, an aftereffect may or may not correlate with awareness, depending on the method used for suppressing visibility.

Inattention might affect adaptation in ways other than suppressing visibility. Attention can increase neural responses to the attended stimuli, improve selectivity, or enhance adaptability (Boynton, 2004). Consequently, aftereffects may be weaker (although still present) when the stimulus is not or only weakly attended during adaptation.

In a second set of experiments, we measured face-adaptation while observers were engaged in an attentional demanding working memory task. Will the face aftereffect be reduced, revealing a residual effect that requires little attention, or even be eliminated?
under this condition? If face adaptation correlates with awareness regardless of the paradigm used for suppression, then it is likely that visual awareness is required for the face-specific aftereffects.

**Results**

Participants were trained to identify four individual, colored faces. Experimental sessions started after observers reached a fixed performance level on a four alternative forced-choice (4-AFC) face identification task (see methods). The average face (defined as the three-dimensional morph — or mean — of a sample of 200 faces of young adults (Blanz and Vetter, 1999)), was presented in the right visual field, and replaced subsequently by the anti-face of one of the original faces (adaptor). After adaptation, a second face (target) briefly appeared in the left visual field, and observers were asked to identify it. Since the adaptor and target did not overlap, the effect of local adaptation is minimized.

Original faces were morphed with the average to create targets with different identity strengths. The original faces have identity strengths of one, and the average face has identity strength of zero. For each individual face, identity strengths between zero and one were obtained by linear interpolation between the original and the average face (Leopold et al., 2001). The anti-face can be thought of as having negative identity strength relative to its associated, matching face (Leopold et al., 2001).

In Experiment 1 (Fig. 1a), the anti-face was always presented to one eye for 4 s. The adapting eye was determined by asking the observer to point a finger to a distant target. The eye that was not aligned with the finger was used for adapting. In half of the trials, a pattern of moving random dots was presented to the other eye and observers were asked to monitor the visibility of the adaptor and press and hold a key whenever it disappeared. In a considerable number of trials the moving pattern completely erased percept of the anti-face, making it invisible (Fig. 1b). After the 4 s presentation interval, the target face was flashed for 200 ms to both eyes followed by a mask (Fig. 1a). In control experiments, we confirmed that during the suppression periods, faces could not be identified, and verified that face aftereffect transfers between the eyes (i.e., the aftereffect does not depend to which eye the adaptor and the target are presented).
Figure 1c depicts identification accuracy as a function of identity strength, with chance performance corresponding to 1 in 4 (0.25). In all conditions, identification of the target improved as identity strength increased. The difference between dashed and solid curves reflects the identity-selective aftereffect of the adapting anti-face. The left plot depicts adaptation in the non-rivalry condition, with a horizontal shift of 0.07±0.01 (p < 0.0001) between dashed and solid curves. When the anti-face adaptor was clearly visible (non-rivalry trials), the corresponding face was identified more frequently compared to non-matching faces. This difference virtually disappears when the adaptor is suppressed by rivalry for more than 3 s (right plot in Fig. 1c, labeled 'Invisible', shift = 0.01±0.01, n.s.). The middle plot ('Partially suppressed') includes all other trials during binocular rivalry (i.e., when the anti-face was suppressed for 0 to 3 s). The two curves are separated by 0.06±0.01 unit identity strength (p < 0.001). Thus, mere presentation of a second stimulus does not seem to affect face adaptation.

Identity thresholds, defined here as the facial identity strength that was correctly identified in half of the trials (Fig. 1d), were estimated by fitting a sigmoid curve to the data for each condition. The threshold for the corresponding face was significantly lower than unrelated face in non-rivalry trials as well as when adaptor was only partially invisible (<3 s). Only six observers that had more than 160 trials with >3 s suppression were included in the invisible condition. The threshold for the corresponding face was the same as the threshold for unrelated faces in the invisible trials. The magnitude of the aftereffect in the non-rivalry and partially invisible trials for these six observers were similar to the rest of the subjects that did not experience suppression in most of the trials (p>0.4).

The difference in threshold increased as a function of the cumulative duration of visibility (Fig. 2a). In Experiment 2, we measured the face aftereffect as a function of adaptation time for fully visible adaptors (Fig. 2b). As expected, the magnitude of the aftereffect depends on the adaptation time, matching the effect of the visibility in Experiment 1.

It could be argued that our particular setup or the choice of rival stimuli block any retinal input from reaching the visual cortex. Therefore, we verified that orientation-selective adaptation is fully retained under our conditions of perceptual invisibility, by using the same setup as Experiment 1 except that the adaptor consisted of slowly drifting
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Face adaptation depends on seeing the face sinusoidal gratings rather than a face. We measured contrast detection threshold of a subsequent Gabor patch with the same spatial frequency of either the same or the orthogonal orientation (Fig. 3a). Thresholds were significantly elevated for the same orientation compared to the orthogonal orientation after adaptation to both visible (non-rivalry) and perceptually-invisible (suppressed > 3 s) gratings (27±5% vs. 28±7%, n.s. between conditions. Fig. 3b). Although suppression – as measured by key press – was even stronger than for faces, binocular suppression did not have any effect on the orientation-selective adaptation.

Thus we established that the face-aftereffect depends on the perceptual visibility of the anti-face, rather than on the duration of the stimulus. In contrast, more low-level aftereffects such as orientation-selective adaptation depend on the physical stimulus rather than the percept (Blake and Fox, 1974).

Experiments 3 and 4 addressed the question whether within, or between modalities competition for attentional resources can suppress identity-specific face processing, including the face aftereffect. When attention is distracted and engaged in a highly demanding task, task-irrelevant stimuli can be suppressed from awareness (inattentional-blindness) (Simons and Chabris, 1999). The anti-face was presented binocularly for 4 s, and observers were required to either passively view the anti-face, or actively attend to a stream of distracters and perform a 2-back memory task (Fig. 4a). In Experiment 3 visual distracters (digits) were presented at fixation. In Experiment 4, distracters were either sinusoidal tones or a recorded voice speaking the digits. Both tasks require attention to non-face stimuli and engage working memory to the same extent. However, memorizing an auditory stream does not necessitate visual competition (Duncan et al., 1997).

Figure 4b depicts the psychometric curves after exposure to the relevant or irrelevant anti-face (Experiment 3). It is not necessary to actively attend to the adapting face to experience the aftereffect (both passive viewing condition and auditory memory task). However, attending to a competing stream of non-face visual distracters presented at the fixation practically eliminated the face-aftereffect. The residual aftereffect is only marginally significant (p = 0.07, one-tailed t-test). The results are compared with Experiment 1 in Figure 4c. Performing the same task with an auditory stream of inputs did not reduce the aftereffect. Although auditory distracters and cognitive load are known
to affect the performance of some visual tasks, cross-modal inattention does not actually suppress visibility (Arnell and Larson, 2002; Duncan et al., 1997). The above findings indicate that subjective visibility (awareness) and adaptation for faces are closely related. In contrast, we observed a significant orientation-specific aftereffect following adaptation to inattented drifting gratings (19±5%, p = 0.01). The magnitude of the orientation-selective aftereffect was comparable to the passive viewing condition (11±5%, p=0.03, n.s. between conditions). Remarkably, the absolute thresholds were higher in the inattented condition compared to the control (p = 0.015, two-tailed t-test) demonstrating that the 2-back memory task interfered with the conscious registration of the subsequent grating.

Adaptation to face identity is presumably driven by bottom-up visual input. To investigate cognitive, top-down contributions to face-adaptation, Experiment 5 measured the effect of mental imagery on identification of subsequent physical faces. Six naïve observers were familiarized with anti-faces and practiced imagining them. In the experimental sessions, observers imagined a particular anti-face for a few seconds before a target was briefly presented which they had to identify. Six observers were instructed to imagine these faces as vividly as possible and report the vividness of their mental picture in each trial. Face imagery has been shown to activate the same brain areas and neurons that are activated by the physical stimulus (Kreiman et al., 2000; O'Craven and Kanwisher, 2000). Yet, imagining an anti-face did not affect the identity threshold for its corresponding vs. unrelated faces (threshold change = 0.007±0.01, p = 0.28), regardless of the clarity of the mental image or the duration of the imagery. Therefore, it is unlikely that the suppression of the face aftereffect in Experiments 1 and 3 can be attributed to a cognitive component.

**Discussion**

Binocular suppression virtually eliminated the face aftereffect whereas it had no effect on orientation-selective adaptation. Other studies provide evidence of aftereffects that do not depend on consciously seeing the adaptor (Blake and Fox, 1974; Lehmkuhle and Fox, 1975; O'Shea and Crassini, 1981; White et al., 1978). These findings indicate that binocular rivalry is resolved after simple features, but before complex stimuli are
represented in the ventral pathway. So far, no other aftereffect originating in the ventral stream has been shown to require visibility.

Like face adaptation, the magnitude of the spiral motion aftereffect is a function of the duration of the dominance period of the adaptor in binocular rivalry (Wiesenfelder and Blake, 1990). This dependence indicates that spiral motion is processed in the visual system beyond binocular interactions. Yet under different circumstances, spiral motion can result in an aftereffect without reaching awareness (Aghdaee, 2004). In this study, the direction of a spiral was made subjectively invisible by crowding, that is, surrounding it with similar spiral flankers. Although the observers failed to resolve and discriminate the direction of the adapting spiral in the crowded condition and reported it at chance level, the aftereffect (measured by presenting an ambiguous spiral afterwards) was preserved (Aghdaee, 2004). The crowding effect occurs when the distance between stimuli are smaller than the resolution of attention, that is, crowding can be considered as a form of inattention. Therefore, the spiral motion aftereffect is preserved under inattentional blindness.

The suppression of face-adaptation under a high attentional load favors a relatively early site for attentional competition within the ventral stream: competition for attentional resources is resolved before face identity-specific processes in FFA. Our results are compatible with the notion that observers’ failure to notice unexpected and irrelevant stimuli in inattentional blindness (Mack and Rock, 1998; Simons and Chabris, 1999) reflects a genuine suppression of such stimuli, rather than a retrospective failure to recall them. Presumably, elimination of the aftereffect is due to the suppression of visual input from reaching face-selective neurons, and not because face processing requires attention. Interestingly, spatial, selective attention is not necessary for face gender or identity categorization (Reddy et al., 2004). Likewise, our results indicate that face adaptation can be obtained under passive conditions. This indicates a dissociation between spatial visual attention and visual awareness. Indeed, we recently demonstrated that the magnitude of BOLD response to peripheral faces does not decrease when observers are engaged in an attentional-demanding central task, as long as observers are aware of the faces (Reddy, Moradi, Koch, VSS 2004).
Our findings are seemingly at odds with reports showing implicit priming (Mack and Rock, 1998) and increased activity in face and scene selective occipitotemporal areas in human observers in the absence of awareness (Marois et al., 2004; Moutoussis and Zeki, 2002). Increased BOLD activity in those studies may reflect an incomplete suppression of stimuli from awareness in those paradigms. Alternatively, it is plausible that priming and an increased BOLD signal in the absence of awareness reflect insufficient neural activity — or different neural populations — to mediate adaptation and conscious registration of the input. FMRI is not necessarily more sensitive than psychophysically measured adaptation to uncover implicit activations: Rees et al. (Rees et al., 1997) reported strong suppression of fMRI activity in the human V5/MT complex but only a modest 23% reduction in the duration of the motion-aftereffect under high attentional-load. Thus, although inattended motion did not produce any measurable BOLD activity in their experiment, it still invoked a measurable aftereffect. Further studies and better control for awareness are necessary to resolve the discrepancy between fMRI studies and adaptation results.

It is possible, that the neural substrate that underlies both conscious face recognition and identity-specific aftereffect is distinct from the substrate that underlies implicit face recognition or other aspects of face perception. Face perception is mediated by a distributed neural system that may involve multiple regions or pathways (Haxby et al., 2001). The amygdala, for example, has been implicated in perception of emotion in facial expression (Young et al., 1996). Interestingly, two recent imaging studies showed activation in amygdala in response to binocularly suppressed images of facial expression (Pasley et al., 2004; Williams et al., 2004). Sporadic residual activation in such a distributed system may explain implicit face recognition in prosopagnosia (de Gelder et al., 2000; De Haan et al., 1992). Nonetheless, our results indicate that adaptation to face identity is specific to the pathways that are affected by inter-ocular suppression and inattention, and shares the same underlying neural substrate with conscious face identification. If configural adaptation to facial expressions involves the same pathway, then it should also depend on visibility. Alternatively, it is possible that adaptation to the emotional expression of a face is preserved for invisible faces.
In summary, our findings establish a close relationship between configural face adaptation (Leopold et al., 2001) and visual awareness. If you don’t see a face, you will not adapt to its identity, even though you may adapt to other aspects of the face such as orientation or color. It appears paradoxical that some aftereffects such as negative afterimage or orientation-dependent aftereffect do not require seeing the inducing stimulus. Contrariwise, the result reported here for the identity aftereffect is more in line with common expectation. Together, these findings provide insight into brain organization and the neural correlates of conscious perception.

**Experimental Procedures**

Healthy, paid volunteers with normal visual acuity were recruited from the campus student population. Participants were naïve to the purpose of the experiment, and were trained to identify four target faces in a 4-AFC task. Auditory feedback was given after each misidentification. Training blocks of 100 trials were repeated until observers performed better than 95% accuracy in training level 1 (identity strengths = 0.3, 0.4), 84% in level 2 (strengths = 0.2, 0.3, 0.4), and 75% in level 3 (strengths = 0.15, 0.25, 0.4). Participants were trained using this protocol at the beginning of each session. We observed that overtraining reduces the face-aftereffect, so for Experiment 4 and 5 observers only completed levels 1 and 2.

Face stimuli were identical to a previous study (Leopold et al., 2001), except that the contrast of the anti-faces were reduced by dividing pixel intensities by two. Our pilot experiments showed that this reduction had little effect on the magnitude of the aftereffect, but it considerably reduced the predominance periods of anti-faces during rivalry.

Stimuli were presented using Matlab Psychophysics toolbox on a PC computer. Participants heads were stabilized using a chin-rest located 80 cm away from the 19” CRT display (resolution = 1027x768, 100 Hz refresh rate). In Experiment 1 we used a mirror haploscope to present images separately to each eye. No feedback on face identification was given in the experimental blocks. Auditory feedback was given in Experiment 3 on the memory task. Visual feedback on the memory task was given after each trial in Experiment 4. We used a loose exclusion criterion based on observers’
performance in the working-memory task (detecting more than half of the repetitions). One participant was excluded each experiment. The orientation-selective adaptation control was carried on seven naïve observers using the same setup as in Experiment 3.

For Experiment 5, participants were trained to associate names to anti-faces. Each trial started with a name followed by a face and observers were asked to report if they match. Incorrect responses were followed by auditory feedback. In the imagery practice session, observers were instructed to imagine the face whose name was displayed briefly for 3-4s and report the vividness of their imagery before the face-to-match was displayed. Participants performed 200-300 practice trials. The experimental session was similar to the practice session, except observers had to identify the target faces after imagining the anti-face.
Figure 1
Face adaptation under dichoptic viewing. a) Twelve observers were exposed to a specific anti-face for four seconds in the adapting eye, while viewing a rotating sphere of random dots in the other eye. Participants were instructed to continuously monitor and report the visibility of the face. After adaptation, they were asked to identify the subsequent face. In the non-rivalry condition (not shown), the other image was blank. b) Histograms of total duration of suppression of the face stimuli for four representing observers (top four histograms), and all twelve pooled observers. c) Psychometric face identification curves after adaptation. The difference between the dashed and solid curves reflects an anti-face specific aftereffect. d) Adaptation to an anti-face decreased the detection threshold of the corresponding face compared to the threshold for unrelated faces in non-rivalry condition, but not when the face was suppressed and invisible for more than 3 s. Partial suppression indicates trials where the anti-face was visible for more than 1 second.

Figure 2
The face aftereffect depends on the duration of predominance of the anti-face. a) We pooled the data of all twelve observers in Experiment 1. A significant aftereffect occurs when the anti-face is visible for more than 1 s. Error bars correspond to s.e.m. b) The time dependence of the face-aftereffect is parallel to the effect of the duration of physical exposure in the binocular setup where the anti-face is always visible (Experiment 2, 5 observers). The threshold change is normalized relative to the group mean of threshold change after 4 s visibility in each experiment. (* p<0.05, *** p<0.001, one-tailed paired t-test).

Figure 3
Orientation-selective adaptation is not affected by binocular suppression. a) Seven observers were first exposed to a grid for 250 ms, followed by two slowly-drifting gratings for four seconds in the adapting eye, while viewing a rotating sphere of random dots (rivalry condition) or blank screen (non-rivalry condition) in the other eye. Participants were instructed to continuously monitor and report the visibility of the
grating. After adaptation, they were asked if the subsequent low contrast grating was in the left or right visual field. b) Adaptation to a particular orientation increased detection threshold for the same orientation compared to the threshold for orthogonal orientation in both non-rivalry and invisible (suppressed > 3 sec) trials. In agreement with previous findings, the orientation of the stimulus can be suppressed from awareness (‘Invisible’), without causing a reduction in the orientation-dependent aftereffect relative to control (‘non-rivalry’).

**Figure 4**

The face aftereffect is reduced under high-attentional load. a) Observers were asked to perform a 2-back memory task during 4 s of adaptation (high-attentional load condition, Experiment 3). A stream of digits appeared at fixation. Observers were required to perform two tasks: the 2-back task during adaptation and the target detection task when the target face appeared. b) Identification curves following adaptation to the corresponding anti-face (dashed) vs. an unrelated face (solid). The two curves are almost identical when observers are engaged in a highly-attentional demanding visual (Experiment 3, 7 naïve observers) -but not the auditory task (Experiment 4, 5 naïve observers). In the “passive viewing” trials observers were not required to carry out any interfering task during the adaptation. c) Summary data comparing the reduction of the face-aftereffect by binocular suppression and with-in and cross-modal attentional load.

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References

Figure 2

![Graph showing threshold vs. duration of visibility of adaptor for corresponding and unrelated faces.](image)

**Normalized Threshold Elevation**

- **Dichoptic (Exp 1)**
- **Binocular (Exp 2)**

- **Threshold**
  - Corresponding face
  - Unrelated face

- **Duration of the visibility of adaptor (s)**
Adaptation (4 s)
Slowly drifting grating,
Contrast = 50%
Blank (300 ms)

Stationary grid (250 ms)
Superposition of 45° and 135° gratings

Adaptation (4 s)
Slowly drifting grating,
Contrast = 50%
Blank (300 ms)

Target (200 ms)

**Figure 3**

A

Suppressing eye
Adapting eye

Stationary grid (250 ms)
Superposition of 45° and 135° gratings

Adaptation (4 s)
Slowly drifting grating,
Contrast = 50%
Blank (300 ms)

Target (200 ms)

B

- Orthogonal orientation
- Same orientation

Detection threshold (% contrast)

<table>
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<tr>
<th>Orientation</th>
<th>Non-rivalry</th>
<th>Invisible</th>
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<td><img src="same_rivalry_graph.png" alt="Graph" /></td>
<td><img src="same_invisible_graph.png" alt="Graph" /></td>
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</table>

p < .005 p < .005
Average face (333 ms)

Adaptation (4 s)

Contrast = 50% of the original

One digit appears every 333 ms

Blank (300 ms)

Target (200 ms)

Mask

Corresponding face

Unrelated face

Identity strength

Proportion correct

Threshold change

p < .005

p < .005

p < .005

p < .005

p = 0.22

(n.s., n=6)

p = 0.07

(n.s., n=7)

p < .005

(n=5)

Experiment 3

Passive viewing (Experiment 3)

High visual attentional load

High auditory load (Experiment 4)

Passive viewing

Experiment 1

Experiment 4

Proportion correct

Threshold change

n.s.

n.s.

n.s.

n.s.

Auditory load

High auditory load (Experiment 4)

Identity strength

 Experiment 3

Figure 4