The temporal decay of eye gaze adaptation effects

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Recent findings demonstrate that the perception of other people’s eye gaze direction can be dramatically biased by previous adaptation to that gaze direction. Here, we further investigated this aftereffect by examining its development over time, with particular attention to the potential role of the ambiguity of the test stimulus. Following adaptation to gaze to one direction, participants’ ability to correctly classify gaze to the adapted direction was severely impaired, both for ambiguous and relatively unambiguous test stimuli. Of particular importance, this aftereffect decreased over time but remained measurable up to 7 minutes post adaptation, with its decline following an exponential decay function. The implications of the present findings are discussed with respect to both coding mechanisms involved in gaze perception and a potential role of adaptation effects in real life situations.

Keywords: face perception, high-level adaptation, figural adaptation, gaze perception, neural habituation, time course


Introduction

Visual adaptation has long been investigated in order to gain insight into the processing mechanisms of the human visual system. Traditionally, visual aftereffects have been studied and reported for early stages of processing and for relatively simple stimulus characteristics such as luminance, contrast (Chen, Zhou, Gong, & Liang, 2005), color, or motion (Antal et al., 2004). One of the most popular and extensively investigated examples is the motion aftereffect (MAE) whose first mention is ascribed to Aristotle (Parva Naturalia). Here, the prolonged viewing of a downward-moving stimulus subsequently leads to the illusionary perception of an upward motion in a static image (Purkinje, 1820; see Anstis, Verstraten, & Mather, 1998, for a review). This phenomenon has been explained to result from a disequilibrium between motion detectors tuned to opposite directions—with neural fatigue (Barlow & Hill, 1963) and reciprocal inhibition processes (Culham et al., 1999; Tootell et al., 1995) being discussed as the underlying neural mechanisms. The observation of this MAE (as one example of a well-established visual aftereffect) therefore revealed detailed and non-invasive insight into the organization of the neural system processing vertical motion—with one subsystem detecting upward motion and a second subsystem detecting downward motion. While adaptation to simple stimulus attributes has been known for literally hundreds of years, a striking novel discovery within the last few years was that adaptation is also of central importance for the perception of very complex visual stimuli. Webster and MacLin (1999) reported the so-called face distortion aftereffect (FDAE)—a figural aftereffect affecting the perception of face configurations. They found that adaptation to distorted (e.g., contracted) faces subsequently led to an altered perception of normal faces: Participants perceived normal test faces as distorted in the direction opposite to adaptation (e.g., expanded). Similar high-level adaptation processes with contrastive aftereffects have also been reported for other face-related processes such as the perception of identity (Leopold, O’Toole, Vetter, & Blanz, 2001), gender (Kovács et al., 2006), viewpoint (Fang, Ijichi, & He, 2007), ethnicity, and emotional expression (Webster, Kaping, Mizokami, & Duhamel, 2004). As in the investigation of adaptation effects for simple stimulus characteristics, figural high-level adaptation experiments with face stimuli allow a valuable insight into the mechanisms and functional organization of face perception: Webster and MacLin (1999), for example, reported the FDAE to be asymmetric, i.e., adaptation to distorted but not to undistorted (“normal”) faces showed a clear effect on the perception of subsequently presented test faces. This is in line with the theory of a so-called “face–space” (Valentine, 1991) which suggests face representations to be organized in a multi-dimensional space with an average face prototype as the center (see also Leopold et al., 2001).

Recent studies suggest that the perception of eye gaze direction in human faces can also be altered by adaptation (Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006). This is an interesting finding as the directional content in eye gaze is an important social signal. Eye gaze is able to evoke attentional shifts in observers (Driver 2006).
et al., 1999; Friesen & Kingstone, 1998; Schuller & Rossion, 2001) at least when processed in foveal vision (Burton, Bindemann, Langton, Schweinberger, & Jenkins, in press), and humans are very efficient in detecting even small (<1° of visual angle) relative changes in the gaze direction of others (Symons, Lee, Cedrone, & Nishimura, 2004). Jenkins et al. (2006) found that adaptation to gaze directed into a certain direction dramatically impaired participants’ subsequent ability to perceive eye gaze in the adapted direction. They presented participants with a series of adaptation stimuli showing faces with gaze universally directed 25° to either the left or right side. Following adaptation, participants typically perceived eye gaze into the adapted direction as looking straight at them. This effect was found to be symmetric, i.e., the influence of adaptation on the perception of gaze into the adapted direction was equivalent for left and right adaptation direction. In a similar study, using a two-alternative forced-choice response setup with “left” and “right” as response options, Seyama and Nagayama (2006) found that after adaptation to eye gaze in one direction participants classified straight eye gaze or gaze directed into the adapted direction more often as pointing into the direction opposite to adaptation. Seyama and Nagayama (2006) also found symmetric results for the adaptation to left and right eye gaze direction. Both Jenkins et al. (2006) and Seyama and Nagayama (2006) conducted a further experiment in order to rule out that the reported aftereffects were exclusively due to low-level adaptation processes (e.g., related to the pupil position). In a third experiment, both groups excluded the hypothesis that the observed gaze adaptation effects were due to general spatial adaptation phenomena independent of eye gaze, suggesting that higher cortical mechanisms selectively code the perception of human gaze directions.

Despite these similarities between studies, there are also some differences in the reports by both groups concerning the nature of gaze direction aftereffects on stimuli gazing in the unadapted direction: In addition to effects of adaptation on eye gaze directed in the adapted direction, Seyama and Nagayama (2006) reported more “left” classifications for straight gaze following adaptation to right gaze and more “right” classifications for straight gaze following adaptation to left gaze (relative to a neutral adaptation condition). By contrast, in their basic experiment, Jenkins et al. (2006) did not report effects of adaptation on the perception of straight gaze or gaze to the unadapted direction. Evidence for aftereffects of gaze adaptation on the perception of unadapted gaze direction is therefore somewhat mixed at present.

High-level face adaptation effects have been detected only in the past few years, and their time course is only just beginning to be studied. Most recently, the effects of different adaptation durations on certain aspects of face perception have been investigated. In a functional magnetic resonance imaging (fMRI) study, Fang, Murray, and He (2007) showed the nature of face adaptation effects to depend on adaptation duration. They reported increasing durations to gradually amplify “viewpoint-tuned” adaptation effects in face-specific areas and found different face-related brain regions to be differentially sensitive to short- and long-term adaptation. Similarly, Kovács, Zimmer, Harza, and Vídy ñ ászky (2007) showed that short-term (500 ms) adaptation effects on face gender perception were invariant to the position of the test stimulus relative to the preceding adaptation stimulus, whereas long-term adaptation (5000 ms) led to facial aftereffects that were characterized by both a position invariant and a position-specific component. Again, these findings suggest that the systematic variation of adaptation durations can be a tool to study selective adaptation of different neural mechanisms of shape-specific coding.

There is relatively little knowledge regarding the nature of the decay of high-level figural aftereffects, whereas the timing parameters of low-level adaptation have been widely investigated and discussed. In general, three important influences on the time course can be distinguished. These aspects are the presentation duration of the adaptor, the presentation duration of the test stimulus, and the time interval between the adaptor and test stimulus. The empirical findings vary considerably across adapted visual properties, the methodological details of the respective experiments, and even across participants. However, generally speaking, the magnitude of most aftereffects increases as a function of adaptation time, and decreases as a function of presentation duration of the test stimulus. For tilt aftereffects, for example, Magnusson and Johnsen (1986) report buildup and decay to be logarithmic functions of time. The duration of motion aftereffects was reported to increase as a power function of the presentation time of the moving adaptation stimulus, while the decline was described by an exponential decay function (e.g., Hershenson, 1989, 1993; see also Petersik, 2002, for a report of an exponential decay for three-dimensional MAEs).

In a first study on the temporal characteristics of high-level face-related adaptation, Leopold, Rhodes, M ü ller, and Jeffery (2005) examined the effects of varying presentation durations of the adaptation (1000 ms to 16000 ms) and test stimuli (200 ms to 1600 ms) on face identity aftereffects. They reported that these aftereffects increase logarithmically as a function of adaptation duration and decrease exponentially as a function of presentation duration of the test stimulus. In a later study, similar findings were obtained for face aftereffects at an even higher (i.e., size-invariant) level (Rhodes, Jeffery, Clifford, & Leopold, 2007).

The present study is motivated in part by the fact that although the influences of adaptor duration and test stimulus duration have been investigated in a few studies, there is only little insight into the influence of the time interval between the presentation of the adaptation and test stimulus on face adaptation effects. Previous studies typically used an adaptor-test interval of just a few hundred milliseconds (Jenkins et al., 2006; Kovács et al., 2006; Leopold et al., 2005; Rhodes et al., 2004; Webster et al., 2004; Webster & MacLin, 1999). The idea that face adaptation effects can survive an interval in the range of
minutes received preliminary support by a brief report (Carbon & Leder, 2006) on a face distortion aftereffect. As a limitation, this study only used one single face (of Mona Lisa) and did not track the decay of the aftereffect. To our knowledge, no study to date precisely evaluated the time course of face adaptation effects as a function of the adaptor-test interval.

In a previous study on the neural correlates of eye gaze adaptation (Schweinberger, Kloth, & Jenkins, 2007), we investigated the effects of adaptation to left and right gaze directions in two consecutive blocks with block order counter-balanced across participants. Although separated by a break that offered a number of intervening visual stimuli (e.g., contact with experimenter, new instruction screen), our data appeared to suggest an influence from gaze adaptors in the first adaptation block on performance in the second block several minutes later. This was an accidental finding that was unrelated to the aims of that study, and that was therefore not reported. As eye gaze direction often changes quickly in real-life situations of human communication, a finding of relatively long-persisting effects of eye gaze adaptation might be somewhat unexpected. In the current paper, we report two experiments specifically designed to gain a systematic evaluation of the time course of eye gaze adaptation effects. In Experiment 1, we measured participants’ ability to correctly identify straight gaze and gaze directed $5^\circ$ left or right, before and directly after adaptation to eye gaze strongly ($25^\circ$) diverted to right direction. In order to monitor the decrease of gaze adaptation aftereffects over time, a series of several further post-adaptation phases was run within approximately ten minutes. As prior research (Jenkins et al., 2006; Seyama & Nagayama, 2006) suggested that the magnitude of gaze adaptation effects partly depends on the ambiguity of the test stimulus, we further explored the role of the ambiguity of test stimuli for the persistence of the adaptation effects: In Experiment 2, we followed the same procedure as in Experiment 1, but using more distinct gaze deviations ($10^\circ$) in the test stimuli.

### Experiment 1

**Methods**

**Participants**

Twenty-five naïve participants (18 to 30 years, $M = 21.6$ years, 3 men) contributed data and received course credit for their participation. They all gave their informed consent and reported normal or corrected-to-normal vision.

**Stimuli**

Test faces were color photographs of 6 male and 6 female young adults as in previous studies (Jenkins et al., 2006). Each model posed at gaze angles of $5^\circ$ left (L05), straight (S00), and $5^\circ$ right (R05; all directions from the observer’s point of view). Photos of the same 12 models gazing $25^\circ$ right (R25) were used as adaptation stimuli. All faces were presented in a black elliptical mask. Test faces measured $13.0 \times 7.5$ cm and adaptation faces measured $19.0 \times 11.0$ cm. Stimuli were presented at a viewing distance of $\sim 87$ cm which was kept constant using a chin rest.

**Procedure**

The experiment began with a **pre-adaptation phase** in order to determine the general ability to accurately perceive the gaze direction of faces. Using right index, middle, and ring fingers on three response keys, participants indicated if a test face showed left, straight, or right gaze direction, respectively. Thirty-six test faces ($12$ identities $\times 3$ gaze directions) were presented in random order. For each trial, a question mark was first presented (800 ms), was then replaced by the test face (400 ms), and followed by a blank screen (2250 ms) during which participants responded. One pre-adaptation trial therefore took 3450 ms, leading to a pre-adaptation phase block duration of two minutes and four seconds (124.2 s).

The pre-adaptation phase was followed by an **adaptation phase** in which participants were presented with two consecutive runs with twelve adaptation stimuli each, presented in randomized order. These stimuli showed eye gaze averted $25^\circ$ in right direction and were passively viewed by participants. Exposure duration was 3500 ms for each adaptation stimulus, with an inter-stimulus interval of 200 ms. Adaptation stimuli were presented at about 150% the size of test stimuli so that the eye regions in adaptation and test stimuli were non-overlapping. The adaptation block had a total duration of one minute and 29 seconds (88.8 s).

The adaptation phase was immediately followed by a series of five **post-adaptation phases** during which participants were again asked to determine the direction of eye gaze. In general, post-adaptation phases were equivalent to the pre-adaptation phase. The first post-adaptation phase, however, was characterized by slight differences in design and duration. Here, each test stimulus was preceded by two consecutive top-up adaptation displays (3500 ms each) presented before the question mark (1000 ms) and the test face (400 ms) to ensure maximal adaptation effects during the whole first test block. To avoid any potential effects of immediate facial identity repetitions (Schweinberger, Huddy, & Burton, 2004), neither of the two top-up adaptation stimuli carried the same identity as the following test face. A single trial in the first post-adaptation block had a duration of 10650 ms—the completion of the whole first post-adaptation phase therefore took 6 minutes and 23 seconds (383.4 s).

Participants were then presented with four further post-adaptation phases that did not contain top-up adaptation
stimuli. The timing parameters of these blocks were equivalent to those of the pre-adaptation phase, with a single trial duration of 3450 ms and a total duration of two minutes and four seconds (124.2 s) for each of the four post-adaptation phases. The consecutive post-adaptation phases were separated by standardized breaks of 30 s each, the first of which was presented immediately after the first post-adaptation phase. At the onset of the first break, participants were informed in writing via the monitor about break duration and were instructed to classify the gaze direction of each face in the following part (as there were no more top-up adaptation stimuli from this point on). All subsequent breaks simply informed the participants about the duration of the break and, 10 s before the end of the break, informed them that they would have to continue with their task shortly. For a short overview of the procedure, please see Figure 1.

The assessment of the temporal persistence of gaze direction aftereffects was a central aim of the current study, and our considerations concerning the analysis of timing were as follows: First, by using top-up adaptation stimuli before each test stimulus, the first post-adaptation phase was designed to capture the maximal adaptation effect in the context of the present study (cf. Jenkins et al., 2006). The starting point in time, relative to which we tracked the decay of aftereffects, therefore coincided with the end of the first post-adaptation phase (see Figure 2). As practical considerations (limited number of participants, randomized presentation of stimuli in different conditions) prevented an assessment of aftereffects on a trial-to-trial basis, we used relatively short test blocks with only 12 test stimuli for each gaze direction in the second to fifth post-adaptation phase. To determine a time course of adaptation effects, we then defined the average time across all test faces within a given phase (relative to the end of the first post-adaptation phase) as a time point of measurement. Similarly, we took the average performance across all test faces within a given phase as an indicator for the residual magnitude of aftereffects at this time. Figure 2 illustrates the resulting time scale.

Data analysis

An analysis of variance (ANOVA) with the factors ADAPTATION PHASE (A00, A01, A02, A03, A04, and A05) and gaze DIRECTION of test stimulus (left, right, and straight) was conducted to analyze the “straight” responses, in analogy to Jenkins et al. (2006). Where appropriate, we performed epsilon corrections for heterogeneity of covariances throughout (Huynh & Feldt, 1976).

Figure 1. Schematic example for trial procedure in the pre-adaptation (first row), adaptation (second row), and 1st post-adaptation (third row) phases. Please note that test stimuli were actually presented at a smaller size than adaptors (see Procedure for details) and that the 2nd to 5th post-adaptation trials were equivalent to the pre-adaptation trials.
All post hoc t-tests were corrected with the Bonferroni-procedure (α = .05).

### Results

In the pre-adaptation test, participants were fairly accurate at discerning eye gaze directions (70.3 ± 22.8%, 71.8 ± 18.9%, and 74.7 ± 18.5% mean correct responses ± standard deviations for left, right, and direct gaze, respectively). As expected, the ability to correctly perceive right gaze direction was strongly reduced after adaptation to that direction (9.8 ± 18.1% correct). The correct classification of straight gaze, however, was relatively unaffected (75.3 ± 15.6% correct responses) whereas correct classifications as “left gaze” appeared to increase after adaptation (e.g., to 83.4 ± 23.2% in the first post-adaptation phase). For the detailed response pattern obtained in the different adaptation conditions (pre-adaptation test, first to fifth post-adaptation test), please see Table 1.

The ANOVA revealed significant main effects of both ADAPTATION PHASE (F(5,120) = 11.42, p < .001) and DIRECTION (F(2,48) = 93.93, p < .001), as well as a significant interaction (F(10,240) = 32.45, p < .001), which revealed that whereas the number of incorrect “straight” responses did not differ for left and right gazing stimuli during the pre-adaptation phase (p > .6), it clearly did so after adaptation: “Straight” responses were significantly more frequent to right as compared to left gazing stimuli from the first post-adaptation phase up to the third one (t(24) = 9.74, p < .001; t(24) = 5.25, p < .001; and t(24) = 3.36, p < .01, for first, second and third post-adaptation phases, respectively). This difference was mainly due to a strong increase of “straight” responses to test stimuli showing right gaze direction after adaptation. Compared to the pre-adaptation phase, there were significantly more “straight” responses to right gazing stimuli in the first (t(24) = 11.87, p < .001), second (t(24) = 6.95, p < .001), and third post-adaptation phase (t(24) = 4.10, p < .001), with a strong trend into the same direction in the fourth post-adaptation phase (puncorrected = .03).

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<th>Direction</th>
<th>Left gaze direction</th>
<th>Right gaze direction</th>
<th>Straight gaze direction</th>
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<td>A05</td>
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Table 1. Mean percentages (±SEM) of left (‘l’), right (‘r’) and straight (‘s’) responses to test stimuli depending on the actual gaze direction of the stimuli (left gaze direction, right gaze direction, straight gaze direction) and the test phase. Please note that the pre-adaptation phase is indicated by “A00,” the first to fifth post-adaptation phases are indicated by the abbreviations “A01” to “A05,” respectively.
Incorrect “straight” responses to test stimuli showing left gaze exhibited a weaker pattern of aftereffects in the opposite direction: Following adaptation to right gaze, incorrect “straight” responses to left gazing test stimuli significantly decreased compared to pre-adaptation level in the first post-adaptation phase only \((t(24) = -3.01, p < .01)\). Although some degree of gradual return to pre-adaptation level could also be observed in the data on left gazing stimuli (see Table 1 and Figure 3), differences to pre-adaptation level were not significant in the other post-adaptation phases.

Concerning the classification of stimuli showing straight gaze direction, there was a very small increase in correct responses after adaptation (see Table 1), which only reached a level of significant difference from the pre-adaptation phase in the third post-adaptation phase \((t(24) = 2.73, p < .05)\). This enhancement was accompanied by a significant decrease in incorrect “right” classifications of straight gazing test stimuli in the first \((t(24) = -3.68, p < .01)\), second \((t(24) = -3.53, p < .01)\), and third \((t(24) = -2.83, p < .01)\) post-adaptation phases.

Figure 3 depicts the mean percentage of “straight” responses to test stimuli gazing left and right against the time elapsed since adaptation. We found that the development of the aftereffect over time for left and right gazing test stimuli could be well defined by exponential functions of the form

\[
    f(x) = (Y_0 - \text{Plateau})e^{-kx} + \text{Plateau}. \tag{1}
\]

Please see Table 2 for an overview of the parameters of the functions fitted for left and right gazing stimuli, respectively.

There was a high goodness of fit of the exponential functions for both the increase in incorrect “straight” classifications of test stimuli showing left gaze \((R^2 = 0.99)\) and the decrease in incorrect “straight” classifications of test stimuli showing right gaze \((R^2 = 0.97)\).

### Discussion

The results of Experiment 1 replicate recent studies on eye gaze adaptation effects (Jenkins et al., 2006; Seyama & Nagayama, 2006; Schweinberger et al., 2007): Prolonged adaptation to faces showing eye gaze directed to the right subsequently led to an altered perception of eye gaze direction. Most strikingly, adaptation biased the classification of eye gaze to the adapted direction to be perceived as direct gaze. This aftereffect decreased over time but remained significant until the fourth post-adaptation phase, corresponding to about 385 s after adaptation (please see Figure 2 for details on the time course). The time course of the aftereffect was well modeled by an exponential decay function (see Figure 3).

As this is the first study to systematically determine the effects of the adaptor-test-interval in high-level face adaptation, it is difficult to relate our findings to those of earlier studies. However, the comparison of the current data with findings on the decay of MAEs suggests a comparatively long-lived nature of gaze adaptation aftereffects. While the exponential nature of the decay function has typically been reported for low-level effects as well (e.g., Hershenson, 1989; Petersik, 2002; Tootell et al., 1995), Hershenson (1989) reported that motion aftereffects induced by extensive adaptation durations as long as 15 minutes almost completely decayed only 80 s after adaptation. We note that whereas the combined effects of adaptor duration and test stimulus duration have been addressed by two previous studies (cf. Leopold et al., 2005; Rhodes et al., 2007), the combined effects of all three factors remain an important issue for future research.

In Experiment 2, we aimed at replicating and extending these findings. We conducted an analogous experiment, however, using less ambiguous test stimuli. As previous studies (Jenkins et al., 2006; Seyama & Nagayama, 2006) showed reduced levels of aftereffects for less ambiguous test stimuli, we hypothesized that those effects might also be subject to faster decay. We therefore determined the decay of adaptation effects for these test stimuli and compared them to those obtained in Experiment 1.

### Table 2

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<th>Parameter</th>
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<th>Right</th>
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<tr>
<td>(Y_0) (in %)</td>
<td>16.17 ± 0.23</td>
<td>84.97 ± 4.76</td>
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<tr>
<td>Plateau (in %)</td>
<td>29.28 ± 0.18</td>
<td>34.87 ± 3.84</td>
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<tr>
<td>(k) (in 1/s)</td>
<td>0.01011 ± 0.00060</td>
<td>0.00954 ± 0.00309</td>
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</table>

Table 2. Parameter estimations for exponential functions fitting percentages of “straight” responses to test stimuli gazing into the left and right direction, respectively. \(Y_0\) represents the intercept (the response at time \(x = 0\)), and the plateau represents the asymptote (the response at time \(x = \infty\)). \(k\) is the rate constant which is expressed in reciprocal of the \(X\) axis time units.
Experiment 2

Methods

Participants

Twenty-five new participants (19 to 32 years old, $M = 21.4$ years, 5 men) contributed data to this study and received course credit for their participation. They all gave their informed consent and reported normal or corrected-to-normal vision.

Stimuli

Test faces were color photographs of the same twelve individuals as in Experiment 1. The models posed at the gaze angles 10° left (L10), straight (S00), and 10° right (R10) leading to a much more obvious deviance from straight gaze in the “left gaze” and “right gaze” conditions as compared to Experiment 1. As before, photos of the same 12 models gazing 25° right were used as adaptation stimuli. Stimuli were of the same size as in the first experiment and a constant viewing distance of ~87 cm was ensured by using a chin rest.

Procedure

The procedure was equivalent to the one in Experiment 1.

Data analysis

An analysis of variance analogous to the one in Experiment 1 was conducted.

Results

Participants showed very good accuracy in discriminating left ($M = 92.9 \pm 14.8\%$), right ($M = 91.3 \pm 16.4\%$), and straight ($M = 88.8 \pm 12.3\%$) gaze directions. These accuracies are much higher than those obtained in Experiment 1 (cf. Table 1), reflecting lower task difficulty. However, even the classification of these relatively unambiguous stimuli was severely altered as a consequence of adaptation, as can be seen in the response pattern depicted in Table 3.

As before, adaptation to stimuli gazing 25° to the right direction severely disrupted the ability to correctly perceive eye gaze into that direction—leading to incorrect “straight” responses in 72.5% ($SD = 17.9\%$) of the trials in the first post-adaptation phase. However, this aftereffect seemed to recover more quickly than in Experiment 1, as incorrect “straight” responses to right test stimuli were already strongly decreased in the second post-adaptation phase ($M = 18.9 \pm 25.2\%$). The ANOVA revealed a significant main effect of ADAPTATION PHASE ($F(5,120) = 74.95$, $p < .001$), a significant main effect of gaze DIRECTION of test stimulus ($F(2,48) = 821.63$, $p < .001$), and a significant interaction ($F(10,240) = 69.62$, $p < .001$). Bonferroni-corrected comparisons showed that the mean percentages of incorrect “straight” responses did not differ for left and right test stimuli during this pre-adaptation phase ($p > .6$). Following adaptation, however, there were significantly more “straight” responses to right as compared to left gazing test stimuli in the first ($t(24) = 16.13$, $p < .001$) and second post-adaptation phase ($t(24) = 3.62$, $p < .01$). These differences between responses to left and right test stimuli were due to a strong increase of “straight” responses to test stimuli showing right gaze direction. Compared to the pre-adaptation phase, there were significantly more “straight” responses to right test stimuli in both the first ($t(24) = 19.18$, $p < .001$) and second post-adaptation phase ($t(24) = 3.02$, $p < .05$). From the third post-adaptation phase on, no such significant post-adaptation effects could be discovered (all $p s > .10$). The percentages of “straight” responses to test stimuli showing left gaze did not differ across adaptation phases (all $p s > .09$).

As in Experiment 1, we plotted the mean percentage of straight responses against the time elapsed since adaptation. The development of the aftereffect over time for right gazing test stimuli could be well defined by an exponential decay function of the form

$$f(x) = (Y_0 - \text{Plateau})e^{(-kx)} + \text{Plateau},$$

with $Y_0$ (in %) = 72.54 ($\pm 1.29$), Plateau (in %) = 8.99 ($\pm 0.76$), and $k$ (in 1/s) = 0.02396 ($\pm 0.00191$). We refrained

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<td>4.7 ± 1.5</td>
<td>2.0 ± 1.0</td>
<td>93.3 ± 2.0</td>
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<tr>
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<td>2.3 ± 2.3</td>
<td>89.2 ± 4.7</td>
<td>8.4 ± 3.6</td>
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<tr>
<td></td>
<td>4.0 ± 1.5</td>
<td>1.3 ± 0.6</td>
<td>94.7 ± 1.7</td>
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<tr>
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<td>1.3 ± 0.8</td>
<td>95.0 ± 1.4</td>
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</table>

Table 3. Mean percentages ($\pm$SEM) of left (“l”), right (“r”), and straight (“s”) responses to test stimuli depending on the actual gaze direction of the stimuli (left, right, straight) and the test phase. Abbreviations as in Table 1.
Experiment 2(dotted lines). comparison with Experiment 1, the functions of both phases (see above). In order to allow for a direct as these did not differ significantly across adaptation from fitting the responses to test stimuli showing left gaze, 

Figure 4

"Straight" responses (%) from fitting the responses to test stimuli showing left gaze, as these did not differ significantly across adaptation phases (see above). In order to allow for a direct comparison with Experiment 1, the functions of both experiments were plotted together in Figure 4. The exponential decay function fit on the “straight” classifications to test stimuli gazing into the right direction almost perfectly matched the empirical data ($R^2 = 0.99$).

As hypothesized, the direct comparison of the results obtained in Experiment 1 and Experiment 2 suggests a much steeper initial decay in the 10° as compared to the 5° experiment.

Discussion

Using less ambiguous test stimuli, the adaptation procedure in Experiment 2 led to a qualitatively similar but reduced perceptual bias in the classification of gaze directions. Immediately after adaptation, test stimuli were most often misjudged as looking straight at the observer—even when in reality showing a substantial 10° gaze deviation into the adapted direction. However, this illusionary aftereffect was only measurable in the first and second post-adaptation phases. Based on the time scale of this study (for details, please see Figure 2), this means that the aftereffect lasted about 77 s. The comparison of the exponential decay functions fitted on the empirical data reveals that apart from the higher initial level of illusions in Experiment 1, there is also a more gradual decrease of these misperceptions in Experiment 1 than in Experiment 2.

General discussion

While the time interval between the adaptor and test stimulus has been previously demonstrated to affect the magnitude of aftereffects following adaptation to simple stimulus characteristics such as motion (e.g., Kanai & Verstraten, 2005), the present study is the first to systematically describe the course of high-level face adaptation effects over time—from their first maximal level until their decay to insignificance. Although aftereffects caused by adaptation to eye gaze direction showed a systematic decay in post-adaptation phases, a remarkable finding of the present study is that such aftereffects were still measurable several minutes post-adaptation. In both experiments, post-adaptation effects (i.e., incorrect “straight” classifications of eye gaze into the adapted direction) were maximal immediately following adaptation, and had decayed to near-baseline levels in the last post-adaptation phase, approximately after ten minutes. In line with previous research (Jenkins et al., 2006; Seyama & Nagayama, 2006), we found the initial level of gaze aftereffects to be smaller for less ambiguous test stimuli. At the same time, adaptation effects on less ambiguous test stimuli were also subject to faster decay.

Previous studies of face adaptation typically used an adaptor-test interval of just a few hundred milliseconds (Jenkins et al., 2006; Kovács et al., 2006; Leopold et al., 2005; Rhodes et al., 2004; Webster et al., 2004; Webster & MacLin, 1999; but see Carbon and Leder, 2006, and Leopold et al., 2001, for informal reports of diminished but still measurable face identity aftereffects after an adaptor-test interval of 2400 ms, and Schweinberger et al., 2008, for novel evidence of auditory adaptation in voice perception lasting for several minutes).

We show that adaptation continues to cause biased gaze perception over several minutes, suggesting that these effects may not be limited to very specific conditions in the laboratory. Instead, it seems likely that, under appropriate conditions, adaptation may bias the social perception of eye gaze in real-life situations. Face adaptation effects have been investigated for a multitude of social signals, some of which are typically subject to relatively rapid changes (e.g., eye gaze direction, expression, facial speech), whereas others (e.g., gender, identity) tend to be more stable over time. Invariant vs. changeable aspects of human faces are thought to be processed in different neural systems (Haxby, Hoffmann, & Gobbini, 2000). A plausible but yet unexplored hypothesis would be that the recalibration processes evident in adaptation effects are faster for those systems coding changeable aspects of facial information. While recent research has begun to demonstrate different mechanisms for short- and long-term adaptation (Fang et al., 2007; Kovács et al., 2007), an important question for future research will be whether both mechanisms and time courses of adaptation effects can be dissociated for different social signals in faces. Tentative support for this assumption might be seen in a comparison of our findings with those by Carbon et al. (2007) who reported residual aftereffects of adaptation to distorted faces to be still measurable 24 hours after adaptation. These authors
measured effects only at one point in time, and a precise tracking of the decay of aftereffects to invariant vs. changeable aspects of faces will therefore be required for a more thorough comparison.

A few studies of adaptation have begun to address the question of contrastive vs. multichannel coding of faces, with some authors reporting evidence for contrastive coding (Leopold et al., 2001; Robbins, McKone, & Edwards, 2007) and others reporting evidence for multichannel coding (Calder, Jenkins, Cassel, & Clifford, 2007). When considering that those studies investigated adaptation to different social signals in faces, those findings are not necessarily in contradiction. The present results might be reconciled with the idea of contrastive (two-channel) coding of horizontal eye gaze direction. We concede that, on the basis of the present data, it is difficult to completely exclude a multi-channel system with separate channels for distinct gaze directions (in the most simple case, left, direct, and right), at least when assuming relatively broad tuning curves of individual channels. However, two aspects of the current data seem to be more in line with the idea of contrastive coding of gaze direction: First, multichannel models predict adaptation effects to mainly arise for test stimuli close to the adaptor (Robbins et al., 2007). Our data, however, show that adaptation to eye gaze deviating by $25^\circ$ causes substantial and more persistent aftereffects for the perception of $5^\circ$ test stimuli as compared to $10^\circ$ test stimuli. Second, unlike the basic results of Jenkins et al. (2006), but similar to Seyama and Nagayama (2006), adaptation to right gaze in the present study not only impaired the observer’s perception of gaze in the adapted direction, but also improved observer’s perception of gaze in the opposite direction, again supporting the idea that adaptation effects to eye gaze reflect the coding of gaze direction in a contrastive manner.

## Conclusion

Based on a recently established paradigm that demonstrated dramatic impairments in the perception of eye gaze to an adapted direction, the present study demonstrates, for the first time, that such aftereffects continue to be measurable for several minutes after adaptation. The decay of adaptation almost perfectly followed an exponential function, with more ambiguous test stimuli producing both a larger initial illusion, and a more gradual decay over time. We conclude that the investigation of the time course of adaptation effects for different types of stable and changeable facial signals may provide important insights into the respective coding mechanisms involved in face perception.

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## References


