Gaze direction aftereffects are surprisingly long-lasting

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Abstract

Adaptation to gaze direction induces aftereffects in the perception of gaze in subsequently presented faces. Gaze adaptation calibrates neural responses to the most frequently occurring gaze signals and therefore frees up capacity to respond to more novel signals, likely enhancing gaze discrimination and supporting novelty detection. The longevity of aftereffects can provide some insight into the temporal window over which this calibration occurs. Since gaze direction is a rapidly changing signal in the face, one might expect gaze aftereffects to also be very short-lived. Here we show that this is not the case. In Experiment 1, we measured participants' aftereffects immediately after gaze adaptation and 24 hours later. We found significant aftereffects at both times. In Experiment 2, we tested whether long-term adaptation also occured when aftereffects were measured only once, 24 hours after adaptation. Again, we found significant long-term aftereffects. These results demonstrate that gaze adaptation can integrate information over remarkably long periods. We discuss the implications of the longevity of gaze direction aftereffects on our understanding of their functionality, and the functionality of face aftereffects more generally.

Keywords: face perception; gaze perception; gaze adaptation; gaze aftereffects; time course

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The face holds cues to a person's identity, sex, ethnic group, approximate age, emotional state, and focus of attention (Calder, Rhodes, Johnson, & Haxby, 2011). Our ability to accurately perceive this variety of information is one of the cornerstones of successful social interactions. The mechanisms that underlie face processing are still not completely understood. However, models of face perception agree in distinguishing between invariant and dynamic face cues, which are thought to be processed by different perceptual mechanisms and in different brain regions (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000). Invariant information is contained in the structural composition of the face and allows us to process the identity, sex, and ethnicity of a person. Dynamic information is based on changes in the muscular activity in the face and provides us with information about a person's gaze direction and emotional state.

Gaze direction is one of the most important communicative signals in the face. It is highly dynamic and can provide us with real-time insight into another person's focus of attention (Langton, Watt, & Bruce, 2000). It also affects our interpretation of the intensity, meaning and personal relevance of other face-related information, such as a person's emotional expression or attractiveness (Adams & Kleck, 2003, 2005; Ewing, Rhodes, & Pellicano, 2010). Moreover, the ability to detect and accurately perceive the gaze direction of others may play an important role in the typical development of a Theory of Mind (Baron-Cohen, 1995).

Gaze perception mechanisms are highly adaptable, as indicated by *gaze direction aftereffects*. For instance, adaptation to faces with unambiguously rightward gaze biases participants to perceive subsequently presented subtle rightward gaze as direct (Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006). The size of gaze aftereffects has been linked with the ability to correctly categorize gaze direction, suggesting a possible functional role in the perception of gaze direction (Pellicano, Rhodes, & Calder, 2013).

Adaptation is not specific to gaze direction perception, but is a common mechanism that affects the neural coding of many different stimulus characteristics, ranging from simple attributes such as colour, motion, and orientation (for reviews, see Kohn, 2007; Webster, 2011) to more complex signals, such as the sex, emotional expression, and identity of faces (for a recent review, see Webster & MacLeod, 2011). It has been suggested that adaptation might be a functionally important mechanism that allows the visual system to “self-calibrate”, that is to flexibly adjust its responses to the distribution of stimulus characteristics that is currently prevalent in our ever-changing visual environment (e.g., Benucci, Saleem, & Carandini, 2013; Clifford, 2005; Gepshtein, Lesmes, & Albright, 2013; Webster, 2011; Webster & Mollon, 1997). Down-regulating the neural response strength to the most frequently occurring stimulus characteristics frees capacity to respond to other stimuli, likely enhancing discrimination of even small differences between stimuli, and supporting novelty detection (Kohn, 2007; Ranganath & Rainer, 2003; Solomon & Kohn, 2014).

Studying the time course of aftereffects can give us some insight into the temporal window over which this calibration occurs. Aftereffects tend to be very short-lived and are typically observed over the range of milliseconds to seconds (Kohn, 2007; Webster, 2011). However, sometimes aftereffects can last much longer. For instance, cataract patients typically experience colour aftereffects for weeks after lens replacement, resulting from adaptation to a cataractous lens, which selectively filters short wavelengths (Delahunt, Webster, Ma, & Werner, 2004). Similarly persistent colour aftereffects can be induced in healthy participants using coloured contact lenses (Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002). These findings suggest that sampling of the colour statistics of the environment to which the visual system adapts can extend over periods as long as weeks.

The time course of the gaze direction aftereffect is largely unknown and to date has only been investigated in a single study (Kloth & Schweinberger, 2008). In that study, the gaze direction aftereffect was measured by comparing participants' ability to discriminate between subtle gaze directions in test faces before vs. immediately after adaptation to a sequence of adaptor faces with obvious rightward gaze. The longevity of this aftereffect was then established by repeatedly testing the perception of gaze direction in test stimuli for another ten minutes (Kloth & Schweinberger, 2008). The aftereffect decayed exponentially, but remained significant up to seven minutes after adaptation, suggesting that it took about seven minutes to overcome the effects of adaptation to a strongly biased gaze direction distribution.

At the time Kloth and Schweinberger (2008) published their results on the longevity of gaze direction aftereffects, other studies seemed to suggest that other face-related aftereffects might be more long-lived than that. For example, Carbon et al. reported face distortion aftereffects for famous faces 24 hours (Carbon et al., 2007), or even a full week (Carbon & Ditye, 2011), after adaptation. In combination with the findings of Kloth and Schweinberger their results seemed to suggest that face distortion aftereffects, which result from adaptation to relatively invariant, i.e., structural, face information, might be more persistent than aftereffects of adaptation to a more dynamic face signal, such as gaze direction.

However, when trying to interpret the longevity of different face aftereffects it is important to consider other possible sources of variation between studies.

Importantly, the studies by Carbon et al. (2007, 2011) and Kloth and Schweinberger (2008) did not only differ with respect to the adapted face signal, but also with respect to details of the adaptation and test procedure. Whereas Kloth and Schweinberger induced the aftereffect and then immediately tested it repeatedly until its decay, Carbon and colleagues induced the distortion aftereffect on one day, and then had participants come back to the lab a day, or a week, later to establish whether perception was still biased relative to a pre-adaptation baseline (Carbon & Ditye, 2011; Carbon et al., 2007). This difference might be important, because repeated exposure to test stimuli can reduce the longevity of face aftereffects (Kiani, Davies-Thompson, & Barton, 2014, see also Jones & Holding, 1975, for similar findings on aftereffects occuring on lower levels of visual processing). Therefore, it is possible that in the absence of repeated testing gaze direction aftereffects might persist over a much longer time scale than suggested by Kloth and Schweinberger's (2008) initial findings, possibly lasting in the range of hours or days, rather than minutes. The present study was designed to test this possibility, by measuring gaze direction aftereffects 24 hours after adaptation, with either a single test to measure the immediate aftereffect (Experiment 1) or no measurement of the immediate aftereffect at all (Experiment 2).

Establishing the longevity of gaze direction aftereffects in the absence of repeated testing will inform understanding of gaze perception, and face perception more generally, in two important ways. First, it will provide insight into the temporal window over which the sampling of the distribution of prevalent gaze directions affects the neural coding of subsequently experienced gaze. Second, studying the persistence of gaze direction aftereffects in a similar paradigm as has previously been used for other, seemingly more long-lived face aftereffects (Carbon & Ditye, 2011;

Carbon et al., 2007; Ditye, Javadi, Carbon, & Walsh, 2013), will provide an opportunity to explore whether the time course of different face aftereffects might indeed be qualitatively different, or whether differences in time course are more likely to be explained by procedural differences.

Experiment 1

In Experiment 1, we established whether gaze direction aftereffects persist over an entirely different time frame than was reported by Kloth and Schweinberger (2008) when the number of tests between adaptation and the final test is dramatically reduced. We measured participants' gaze discrimination performance for small gaze deviations before, immediately after, and 24 hours after adaptation to faces with obviously rightward gaze. We expected significant immediate aftereffects, i.e., a decrease in accurate discriminations of subtle rightward gaze directions immediately after adaptation to faces with rightward gaze (relative to the pre-adaptation baseline) (cf., Calder, Jenkins, Cassel, & Clifford, 2008; Jenkins et al., 2006; Kloth & Schweinberger, 2008, 2010; Schweinberger, Kloth, & Jenkins, 2007; Seyama & Nagayama, 2006). The important question, however, was whether a residual gaze direction aftereffect would still be evident in a second post-adaptation test 24 hours after adaptation. The experimental procedure is similar to that of Carbon et al. (2007), with the exception that we did include one immediate post-adaptation phase in addition to the long-term post adaptation test. The purpose of the immediate post-adaptation test was to ensure that our adaptation procedure was successful in inducing the classic gaze direction aftereffect. The post-adaptation test 24 hours later was run to establish whether this effect still persisted a whole day after adaptation.

Method

Participants. Nineteen Caucasian adults (4 men, 20-36 years, $M = 26 \pm 5$) participated. Data from four participants were excluded due to poor discrimination of subtle rightward gaze in the baseline phase (less than 66% correct discrimination of 5° rightward gaze, corresponding to correct gaze direction perception in less than 8 out of the 12 trials)[1]. The 15 remaining participants (2 men) had an age range of 20-36 years ($M = 27 \pm 5$). They all self-reported normal or corrected-to-normal vision and were naïve to the purposes of the experiment. Written informed consent was obtained from all participants before the study. The experimental procedure was approved by the Human Research Ethics Committee of the University of Western Australia.

Stimuli. The stimulus set was based on photographs of six young male and six young female faces used in previous research (Calder et al., 2008; Jenkins et al., 2006). Each model posed at six different gaze directions. Pictures of faces with 10° leftward, 5° leftward, direct, 5° rightward, and 10° rightward gaze were used as test stimuli. Pictures of faces with 25° rightward gaze were used as adaptor stimuli. Adaptor stimuli measured 6.6° x 10.8°. Test stimuli were presented at 75% the size of adaptors.

Procedure. The experiment took place on two consecutive days[2]. On the first day, participants first completed a *baseline phase,* in which they classified the gaze direction of 60 individually presented test stimuli as left, direct, or right (Figure 1a). Each of the twelve identities was presented at five gaze deviations: 10° leftward, 5° leftward, direct, 5° rightward, 10° rightward. The order in which faces were presented was pseudo-randomized to avoid immediate repetitions of the same identity. Each test stimulus was presented for 400 ms, followed by a blank screen that was presented until a response was made. Participants indicated whether gaze was directed to their left, directly at them, or to their right by pressing one of three labeled keys. In the following *adaptation phase*, each of the 60 test stimuli was presented again, this time preceded by four adaptor faces with 25° rightward gaze. Within each trial, there were always four different adaptor identities, which were all different from the identity of the test face. Adaptors were presented for 2000 ms each, separated by blank screens that were presented for 200 ms. After the presentation of the fourth adaptor, a blank screen of 150 ms preceded the presentation of the test stimulus, which was on the screen for 400 ms and whose gaze direction participants had to classify (Figure 1b).

Over the course of the adaptation phase, 240 adaptors (four adaptors for each of the 60 test faces) were presented for 2 seconds each, resulting in an overall adaptation duration of 8 minutes. To help ensure good attention to adaptor stimuli throughout the experiment, a small asterisk appeared on the centre of the screen during one of the interstimulus intervals between adaptors on half of the adaptation trials. The presence or absence of the asterisk had to be reported at the end of each trial, after participants had indicated the gaze direction of the test face (cf., Rhodes et al., 2015). On the second testing day, the procedure of the baseline phase was repeated.

Please insert Figure 1 about here.

Results and Discussion

Figure 2 shows the proportions of “left”, “direct”, and “right” responses participants made to test faces with different gaze directions during baseline vs. immediately after adaptation (Figure 2a) as well as during baseline vs. 24 hours after adaptation (Figure 2b). Visual inspection suggests that adaptation to rightward gaze induced a general leftwards shift in participants’ perception of gaze direction of subsequently presented test faces (Jenkins et al., 2006; see also tables 1 and 2 in Kloth & Schweinberger, 2008). Most importantly, adaptation to 25° rightward gaze induced a substantial reduction of correct “right” classifications of test faces with 5° and 10° rightward gaze, accompanied by an increase in “direct” responses. Test faces looking straight ahead were more often falsely judged as looking leftward after adaptation compared to baseline, at the expense of a substantial reduction in correct “direct” responses. Finally, test faces looking leftwards were more often correctly classified, and received less incorrect “direct” responses, after than before adaptation (Figure 2a). Again in line with earlier research, it appears that these effects were generally larger for the more ambiguous 5° than 10° test stimuli (e.g., Jenkins et al., 2006). This overall pattern of effects, although reduced, was still evident 24 hours after adaptation, at least for the most ambiguous test faces with subtle gaze deviations (Figure 2b).

Please insert Figure 2 about here.

For statistical analysis, we calculated aftereffects for test stimuli with 5° rightward and 10° rightward gaze by subtracting the proportion of “right” responses after adaptation from the proportion of “right” responses during baseline. An aftereffect of zero indicates that adaptation did not affect the accuracy of gaze direction perception. A positive aftereffect score indicates that adaptation decreased the accuracy of gaze direction perception for stimuli gazing in the adapted direction, with larger differences indicating larger aftereffects. We calculated aftereffects immediately after adaptation and on the next day (both relative to the baseline established on the first day). To establish whether adaptation significantly biased gaze direction perception, aftereffect scores for test stimuli with 5° and 10° rightward gaze were tested against zero using single sample *t* tests. To compare the magnitude of the aftereffect for 5° and 10° test stimuli, paired-sample *t* tests were calculated. Two-tailed tests were used throughout.

Immediate aftereffects. As expected, aftereffects were significantly larger than zero for both 5°, $t(14) = 21.62$, $p < .001$, Cohen's $d = 11.16$, and 10° test stimuli, $t(14) = 5.86$, $p < .001$, Cohen's $d = 3.03$. Aftereffects for test stimuli with 5° rightward gaze ($M = .76$, $SD = .14$) were significantly larger than aftereffects for test stimuli with 10° rightward gaze ($M = .42$, $SD = .28$), $t(14) = 3.94$, $p = .001$, Cohen's $d = 1.02$. (Figure 3a) (cf., Kloth & Schweinberger, 2008).

Long-term aftereffects. Twenty-four hours after adaptation, aftereffects remained significantly larger than zero for test stimuli with 5° rightward gaze ($M = .12$, $SD = .14$), $t(14) = 3.37$, $p = .005$, Cohen's $d = 1.74$. These were significantly larger than aftereffects for test stimuli with 10° rightward gaze ($M = .00$, $SD = .04$), $t(14) = 3.08$, $p = .008$, Cohen's $d = 0.79$, which were not significantly different from zero, $t(14) = 0$, $p = 1.0$, Cohen's $d = 0$ (Figure 3b).

Please insert Figure 3 about here.

These results clearly reveal significant gaze direction aftereffects on day 2, that is, a full 24 hours after adaptation. What exact mechanisms might explain this remarkable longevity? We consider three possible explanations. First, the aftereffect observed on day 2 might be a stored aftereffect from day 1, which would suggest that under some conditions gaze direction aftereffects can survive a whole day. Second, the adaptation procedure on day 1 might have left the adapted channels more susceptible to re-adaptation on day 2. Such a mechanism might have led to selective re-adaptation to rightward gaze during the test sequence on day 2, such that the test stimuli with 5° and 10° rightward gaze might have induced a new aftereffect. Third and finally, it is possible that gaze adaptation only affected participants' perception of gaze direction on day 1, and that on day 2 they simply remembered and reproduced a similar response pattern to the one given the day before.

We first consider how to distinguish between the first two possibilities, that is, whether the significant aftereffects observed for test stimuli with 5° rightward gaze on day 2 are stored aftereffects from day 1 or whether they are induced during testing on day 2. In the latter case, they should build up during testing, and thus be larger in the second than the first half of day 2's testing session. However, if they are a residual aftereffect from day 1, then they should be identical for the two halves, or perhaps larger for the first than the second half. To distinguish the two accounts, therefore, we compared the size of the aftereffect for the first and second half of the day 2 test trials.

To this end, we calculated separate aftereffect scores for the first six test stimuli with 5° rightward gaze and the last six test stimuli with 5° rightward gaze presented on day 2, by subtracting the proportion of "right" responses for each of these sets of trials from the proportion of "right" responses participants had made to test stimuli with 5° rightward gaze during baseline. Aftereffects were significantly larger for the first six (M = .19, SD = .19) than the last six test faces with 5° rightward gaze (M = .04, SD = .12), $t(14) = 3.76$, $p = .002$, $d = 0.97$. This pattern is more consistent with a residual aftereffect decaying over the course of the test session, than a re-adaptation effect that one would expect to build up over the course of the test phase.

It is impossible to rule out the third potential explanation based on the present data alone. That is, participants might have only experienced a perceptual aftereffect on day 1, and then reproduced their response pattern from day 1 on day 2. However, this account would be ruled out if gaze aftereffects occurred on day 2 even when they were not measured on day 1 (cf., Carbon et al., 2007). Under these conditions, significant long-term aftereffects could not be explained by memory or response priming effects, but would instead point towards a stored perceptual aftereffect from day 1.

Experiment 2

Experiment 1 showed that adaptation to rightward gaze still biased participants' gaze perception 24 hours later, suggesting that gaze aftereffects can survive at least a whole day. In Experiment 2 we sought to replicate this finding with a new sample of participants. Moreover, we omitted the immediate post-adaptation phase from the procedure and only tested for aftereffects 24 hours after adaptation. Experiment 1 clearly demonstrated that our adaptation procedure was able to induce immediate aftereffects, allowing us to test for long-term gaze adaptation aftereffects under the same conditions as Carbon et al. (2007) in Experiment 2.

An additional benefit of the modified procedure is that it allows us to examine the possibility that the long-term gaze perception bias merely indicates motor priming or participants consciously trying to remember and reproduce their post-adaptation responses from day 1. If the long-term effect observed in Experiment 1 resulted from response priming or explicit reproduction of the response pattern from day 1, there should be no such effect in Experiment 2. However, if the long-term effect found in

Experiment 1 represents a stored perceptual gaze direction aftereffect it should also be observed in Experiment 2.

Method

Participants. Thirty-two Caucasian adults (14 men, 17-52 years, $M = 23 \pm 10$) participated. Data from twelve participants were excluded from the analysis due to their poor discrimination of subtle rightward gaze in the baseline phase (less than 66% correct discrimination of 5° rightward gaze, corresponding to correct gaze direction perception in less than 8 out of the 12 trials). Two of these twelve participants also failed to meet this criterion for faces with 10° rightward gaze. The remaining 20 participants (10 men, 17-46 years, $M = 21 \pm 7$) self-reported normal or corrected-to-normal vision and were naïve to the purposes of the experiment. None of these participants had taken part in Experiment 1. Written informed consent was obtained from all participants before the study.

Stimuli. The same stimuli as in Experiment 1 were used.

Procedure. Like Experiment 1, Experiment 2 took place on two consecutive days[3]. On the first day, participants completed a *baseline phase* that was equivalent to the one in Experiment 1 (Figure 1a). The following *adaptation phase* was modified from the adaptation sequence of Experiment 1 by replacing the test stimuli with blank screens (Figure 1c). Therefore, participants were only presented with the 25° rightward gaze adaptation stimuli, without seeing any test stimuli or having to make any gaze direction judgments to these faces. As in Experiment 1, adaptors were presented for 2000 ms each, separated by blank screens that were presented for 200 ms. To ensure good attention to the adaptors, a small asterisk appeared on the centre of the screen during one of the interstimulus intervals between adaptors on half of the adaptation trials. After the presentation of the fourth adaptor, a long blank screen interval followed (replacing the presentation of the test stimulus and response screen in Experiment 1), after which participants were prompted to indicate whether the adaptation sequence had contained an asterisk or not. On the second testing day, the procedure of the *baseline phase* was repeated, i.e., this was the first time participants had to make gaze direction judgments after adaptation.

Results and Discussion

Figure 2c summarizes the proportions of “left”, “direct”, and “right” responses participants made to test faces with different gaze directions during baseline vs. 24 hours after adaptation. Visual inspection and comparison with the long-term aftereffect data observed in Experiment 1 (Figure 2b) suggest a qualitatively and quantitatively similar pattern. As in Experiment 1, we calculated the long-term aftereffects for test stimuli with 5° rightward and 10° rightward gaze by subtracting the proportion of “right” responses obtained on day 2 from the proportion of “right” responses obtained during the baseline phase on day 1.

Long-term aftereffects. Aftereffects measured 24 hours after adaptation were significantly larger than zero for both 5°, $t(19) = 2.10$, $p = .049$, $d = 0.94$, and for 10° test stimuli, $t(19) = 2.18$, $p = .042$, $d = 0.97$. Aftereffects for faces with 5° rightward gaze ($M = .09$, $SD = .19$) were numerically larger than aftereffects for faces with 10° rightward gaze ($M = .02$, $SD = .03$), but the difference was not significant, $t(19) = 1.70$, $p = .11$, Cohen’s $d = 0.38$. (Figure 3c).

As in Experiment 1, we ran an additional analysis to establish whether aftereffects were larger in the first half or the second half of the test session on day 2. Aftereffects were numerically, but not significantly, larger for the fist six ($M = .10$, $SD = .19$) than the last six test faces with 5° rightward gaze ($M = .07$, $SD = .24$), $t(19) = 0.68$, $p = .51$, Cohen’s $d = 0.15$. Nor were aftereffects for test stimuli with 10°

rightward gaze significantly different between the first (M = .00, SD = .02) and second half of the test session on day 2 (M = .02, SD = .05), $t(19) = 1.83$, $p = .08$, Cohen's d = 0.41. This pattern is more consistent with a stored aftereffect than a re-adaptation effect that one would expect to build up over the course of the test phase.

In short, Experiment 2 replicated the main findings of Experiment 1. Participants showed significant biases in gaze perception a full day after adaptation. The fact that the modified experimental procedure of Experiment 2 also led to long-term biases in gaze perception rules out motor priming or memory effects as alternative explanations for the effects. Instead, the results strongly suggest that participants in Experiments 1 and Experiment 2 experienced long-term perceptual gaze direction aftereffects that survived a whole day.

Combined analysis of Experiments 1 and 2

To directly compare data between the two experiments, we ran an additional ANOVA on the long-term aftereffects measured on day 2, with Gaze deviation (5° rightward, 10° rightward) as a within-participants factor and Experiment (Experiment 1, Experiment 2) as a between-participants factor. There was only a significant main effect of Gaze deviation, $F(1,33) = 10.67$, $p = .003$, $\eta_p^2 = .24$, indicating a larger aftereffect for test faces with 5° rightward gaze than test faces with 10° rightward gaze. There was no significant main effect of Experiment, $F(1,33) = 0.09$, $p = .76$, $\eta_p^2 = .003$, and no interaction of Gaze Deviation and Experiment, $F(1,33) = 0.76$, $p = .39$, $\eta_p^2 = .022$. Aftereffects were significantly larger than zero for faces with 5° rightward gaze (M = .10, SD = .17), $t(34) = 3.63$, $p = .001$, Cohen's d = 1.23, but not for faces with 10° rightward gaze (M = .01, SD = .04), $t(34) = 1.44$, $p = .16$, Cohen's d = 0.49.

General Discussion

We present the first evidence that gaze direction aftereffects can survive at least a whole day. Across two experiments, the perception of gaze direction was still significantly affected 24 hours after adaptation. The persistence of the aftereffect is remarkable, considering that gaze direction is an immensely dynamic signal, and one might expect any adaptation-induced calibration of gaze coding to also be very transient. Instead, our findings indicate that the neural coding strategies that underlie the perception of gaze update relatively slowly and can still show effects of adaptation to gaze directions that were experienced 24 hours before.

Importantly, participants exhibited long-term gaze aftereffects irrespective of whether or not an initial aftereffect was measured on day 1. This finding rules out response priming or memory effects as possible alternative explanations for the long-term gaze perception biases we report here. Instead, the independence from response requirements, as well as the nature and magnitude of the overall response pattern observed in both experiments (Figure 2b and 2c) strongly point towards a long-term perceptual gaze direction aftereffect.

When considered in combination with the results of the only prior study on the time course of gaze aftereffects (Kloth & Schweinberger, 2008), our data suggest that the persistence of gaze direction aftereffects is not only influenced by the time that passed since adaptation but also by the nature and frequency of intervening visual stimulation. Kloth and Schweinberger continuously tested gaze direction perception in a series of four repeated test blocks for more than ten minutes after adaptation. Under these conditions, the gaze direction aftereffect lasted for about seven minutes, and then it was gone. Here we show that gaze direction aftereffects can survive a whole day when there is no such repeated testing immediately after adaptation. These findings are in line with a recent study that established the effect of intervening test faces on the decay of face distortion aftereffects, albeit over a much shorter time scale (Kiani et al., 2014). Aftereffects declined with increasing adaptor-test delays, and the speed of this decline was accelerated when other faces were presented between adaptor and test (see Jones & Holding, 1975, for similar findings on the decay of low-level aftereffects).

It is striking that natural face encounters between the two testing sessions did not seem to affect the decay of the aftereffect in the same way as the repeated presentation of test faces in a single testing session (Kloth & Schweinberger, 2008). We believe that this may be due to the combined effects of differences in task demands and in the nature of the intervening stimuli. First, participants in our study did not have to explicitly categorize the gaze direction of the faces they naturally encountered between adaptation and test. By contrast, participants in the study of Kloth and Schweinberger were instructed to categorize the gaze direction of the repeatedly presented test faces. This explicit task likely engaged participants' previously adapted gaze perception system much more intensely, and might therefore have contributed to its faster recovery from adaptation, compared to the participants in the present study. Attention enhances adaptation (Rhodes et al., 2011), and it is plausible that increased attention to potentially de-adapting stimuli would also amplify recovery from adaptation.

Second, the repeated test stimuli presented to participants in Kloth and Schweinberger (2008) were the same identities as the adaptors and were also similarly sized (test faces were only about 25% smaller than adaptors). In contrast, the naturally occurring faces seen between day 1 and day 2 by participants in the present study would have been different identities from the stimuli in the study and would have covered a much wider range in size, with some of them much smaller and others much larger than the adaptors. Face aftereffects, for instance emotion aftereffects, are often significantly stronger when adaptors show the same identity as the test faces, and are reduced when the identity of the adapting face is different from the test face (Fox & Barton, 2007; Lai, Oruc, & Barton, 2012; Vida & Mondloch, 2009). Similarly, although face aftereffects do survive size changes between adaptor and test, they are typically reduced by a size change, indicating a size-selective component (Zhao & Chubb, 2001). Therefore, it is possible that the repeated presentation of test identities that match the adapting identities and that are relatively similar in size is more powerful in resetting the gaze direction aftereffect than exposure to faces of other identities and in various sizes, like the ones our present participants would have naturally encountered.

In addition to the nature and frequency of visual stimulation after adaptation, the amount of time spent adapting seems to be an important factor for the longevity of aftereffects. Even small increases in adaptation duration can have substantial effects on the persistence of aftereffects. For instance, Wolfe and O’Connell (1986) observed that two minutes of tilt adaptation elicited an aftereffect that decayed almost completely within four minutes, whereas four minutes of adaptation induced an aftereffect that lasted over two weeks. They suggested that adaptation duration might generally affect the nature of the induced change, with shorter adaptation leading only to short-term fatigue and longer adaptation also resulting in long-term structural changes. Aftereffects in the present study were induced by 8 minutes of adaptation, while participants of Kloth and Schweinberger (2008) only adapted for about 5.5 minutes. Considering Wolfe and O’ Connell’s (1986) findings, it is possible that the longer adaptation duration used in the present study might have induced both short-lived neural fatigue and also more persistent structural changes, whereas the shorter adaptation duration of Kloth and Schweinberger (2008) might have primarily induced short-lived fatigue effects.

We found significant long-term gaze aftereffects for test faces with 5° rightward gaze in both experiments. For faces with 10° rightward gaze long-term aftereffects were only significant in Experiment 2. The more short-lived nature of the aftereffect for faces with 10° gaze might be related to the smaller initial aftereffect size for these stimuli. With equivalent decay rates, one would expect smaller aftereffects (e.g., for 10° test faces) to reach baseline performance levels sooner than larger aftereffects (e.g., for 5° test faces). Moreover, there is evidence that aftereffects for 10° test stimuli actually decay more rapidly than aftereffects for 5° stimuli (Kloth & Schweinberger, 2008), which would result in them reaching baseline levels even sooner. Considering the smaller initial aftereffects and steeper decay rate for faces with 10° gaze compared to faces with 5° gaze, it is remarkable that there were indeed significant long-term aftereffects for test stimuli with 10° rightward gaze in Experiment 2. It seems possible that the additional (immediate) post-adaptation testing phase in Experiment 1, which was absent in Experiment 2, might have contributed to faster decay of the aftereffect for faces with 10° rightward gaze in Experiment 1 than Experiment 2. We note, however, that the combined analysis of experiments did not provide strong support for this idea. Instead, it confirmed that the overall pattern of effects was very similar in Experiments 1 and 2, with long-term aftereffects for faces with 10° rightward gaze being very small at best and not being significantly different from zero when analyzed across studies.

Kloth and Schweinberger (2008) related their finding that gaze direction aftereffects seemed to persist for only seven minutes to studies showing that face distortion aftereffects for familiar faces seemed to survive days or even weeks (Carbon & Ditye, 2011; Carbon et al., 2007) and suggested that different face aftereffects might decay over completely different time frames. They speculated that the recalibration processes evident in face aftereffects might be faster for those systems coding changeable aspects of face information, such as gaze direction, and slower for those coding more invariant face information, such as the structural composition of faces which is adapted to in face distortion aftereffects (Kloth & Schweinberger, 2008, for possible mechanisms that could explain systematic differences in the time course of different aftereffects, see Bao & Engel, 2012; Bao, Fast, Mesik, & Engel, 2013; Mesik, Bao, & Engel, 2013). The present results strongly challenge this idea. Instead, they demonstrate that adaptation to a facial signal as dynamic as gaze direction can also result in very long-lived aftereffects. Considered in combination with the results of Kloth and Schweinberger (2008) this finding suggests that the time course of aftereffects for the same facial signal can vary substantially, possibly depending more on the nature of the adaptation procedure and the frequency with which relevant faces are encountered after adaptation than on the stimulus characteristic being adapted to.

The longevity of configural face aftereffects reported by Carbon and colleagues might play a functional role in familiar face perception, helping us maintain constancy of identity representations of familiar faces despite natural changes in their appearance. Gaze adaptation also seems to be beneficial to gaze perception. Short-term (immediate) gaze aftereffects have been linked to gaze discrimination ability, consistent with a functional role for gaze adaptation in processing this important facial signal (Pellicano et al., 2013). But what is the functional significance of the long-lasting gaze aftereffects observed here?

We propose that long-lasting gaze adaptation might have a very general functionality. It has been suggested that an important function of adaptation is to calibrate the visual system, that is, to adjust its neural responses to the stimulus characteristics it is exposed to (Clifford, 2005; Webster, 2011). This process ensures constancy in the response distribution across neurons in the visual system despite changes in the distribution of stimulus characteristics (Benucci et al., 2013; Gepshtein et al., 2013; Ullman & Schechtman, 1982). In the present experiments, the adaptation procedure on day 1 induced a strong bias in the diet of sampled gaze directions. This imbalance initiated a recalibration of the response distribution across gaze direction-sensitive channels, which was evident in the behavioural aftereffect. The long-lived nature of this aftereffect implies that the sampling used to calibrate neural responses to prevailing stimulus inputs can occur over extended time windows. Such sampling would be useful because it yields more accurate estimates of the statistics (mean, range, etc.) of an input distribution than more time restricted sampling.

The present results suggest that even for a highly dynamic signal like gaze direction, recalibration can be based on sampling over relatively long windows, at least 24 hours, and may therefore accrue the benefits of extended sampling. It is possible that such an extended time window of sampling is particularly beneficial for the coding of very changeable signals. For signals that are less likely to change from moment to moment, for instance the sex or identity of faces, encounters in the relatively recent past might be quite accurate predictors of future experiences, and adaptation to relatively recent exposure may be sufficient to ensure efficient neural coding. For more changeable signals, very recent exposure may less accurately predict future visual input, and it might be more appropriate to fine tune the response properties of the visual system towards the central tendency of the stimulus characteristics experienced over a longer time frame.

A potential limitation of our study is that we had to exclude data from a relatively large number of participants based on their poor baseline ability to discriminate subtle (5°) rightward gaze. With the gaze direction aftereffect defined as the difference between baseline and post-adaptation gaze discrimination performance, it is simply not possible for a person with poor baseline gaze perception to demonstrate an aftereffect and, therefore, we cannot assess the persistence of the aftereffect in such a person. This problem is common to all research on gaze direction aftereffects. Nevertheless, it suggests that caution may be needed in generalizing our results beyond people with reasonably good gaze perception abilities.

In summary, we demonstrated for the first time that gaze direction aftereffects can survive at least a whole day. Adaptation to faces with 25° rightward gaze induced large immediate aftereffects in the perception of more subtle rightward gaze that still persisted, albeit reduced, when participants returned to the lab 24 hours after adaptation. These long-term aftereffects were found in two experiments, and occurred independently of whether or not the aftereffect was also measured immediately after adaptation, ruling out accounts based on memory or priming of responses to test stimuli. These results strongly suggest that at least under some conditions even adaptation to social signals as dynamic as gaze direction may recalibrate very slowly.

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Footnotes

[1]Gaze direction aftereffects are indicated by a decrease in correct gaze direction perception from subtle gaze deviations in the adapted direction relative to pre-adaptation baseline. Accordingly, only participants that show good baseline discrimination of the adapted gaze direction can potentially demonstrate an aftereffect.

[2]Mostly, the testing sessions took place exactly 24 hours apart. However, three participants were unable to come back after 24 hours, their second test session took place 48 hours after the first. Across the 15 participants, the number of hours between testing sessions ranged from 24 to 48 hours (M = 28.8, SD = 10).

[3]Mostly, the testing sessions took place exactly 24 hours apart. Across the 20 participants, the number of hours between testing sessions ranged from 22 to 24 hours (M = 23.8, SD = 0.5).

Figure 1. a) Baseline procedure as used in Experiment 1 and Experiment 2. Test stimuli were presented for 400 ms each, followed by blank screens. b) Adaptation procedure used in Experiment 1. Test stimuli were preceded by four adaptors with 25° rightward gaze, separated by blank screens. c) Adaptation procedure used in Experiment 2, in which no test stimuli were presented after adaptation. Not shown here is the prompt “Asterisk?”, which was presented as the last item of the adaptation procedure, after the response to the test stimulus (Experiment 1) or the series of blank screens after the last adaptor (Experiment 2). For copyright reasons the depicted identities are different from those used in the actual experiment.

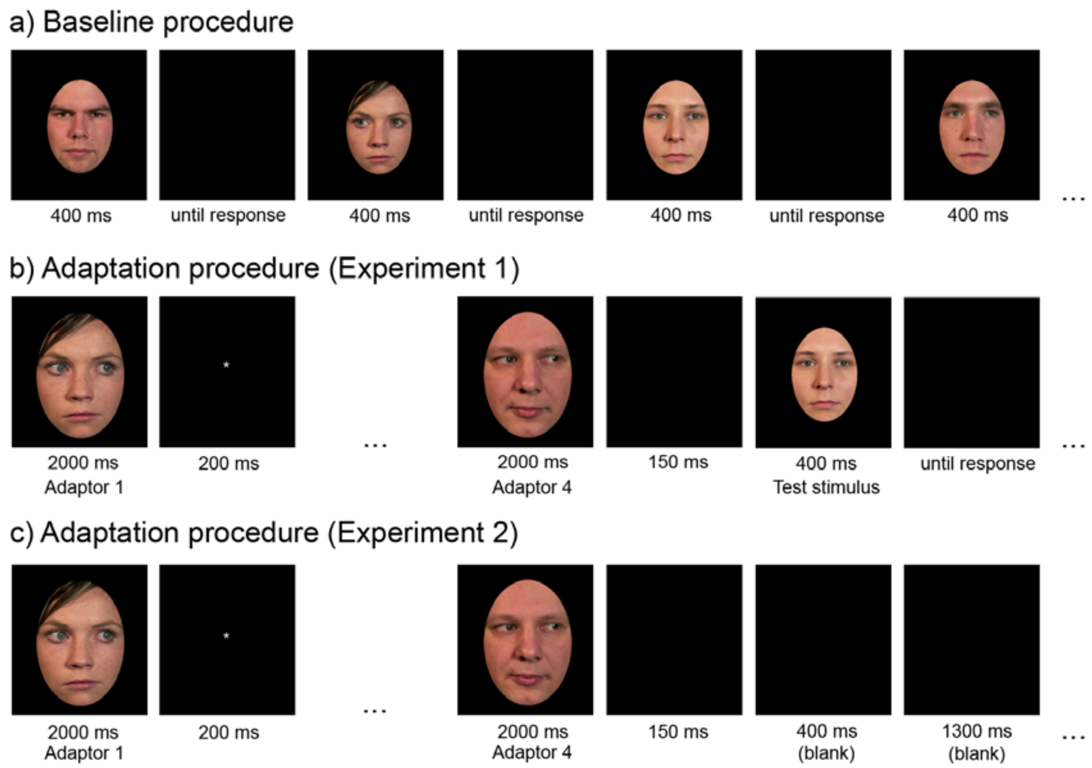

Figure 2. Mean proportions of “left”, “direct” and “right” responses to test stimuli obtained in Experiment 1 a) during baseline vs. immediately after adaptation and b) during baseline vs. 24 hours after adaptation. c) Mean proportions of “left”, “direct” and “right” responses to test stimuli obtained in Experiment 2 during baseline vs. 24 hours after adaptation. Error bars indicate *SEM*s. * $p < .05$.

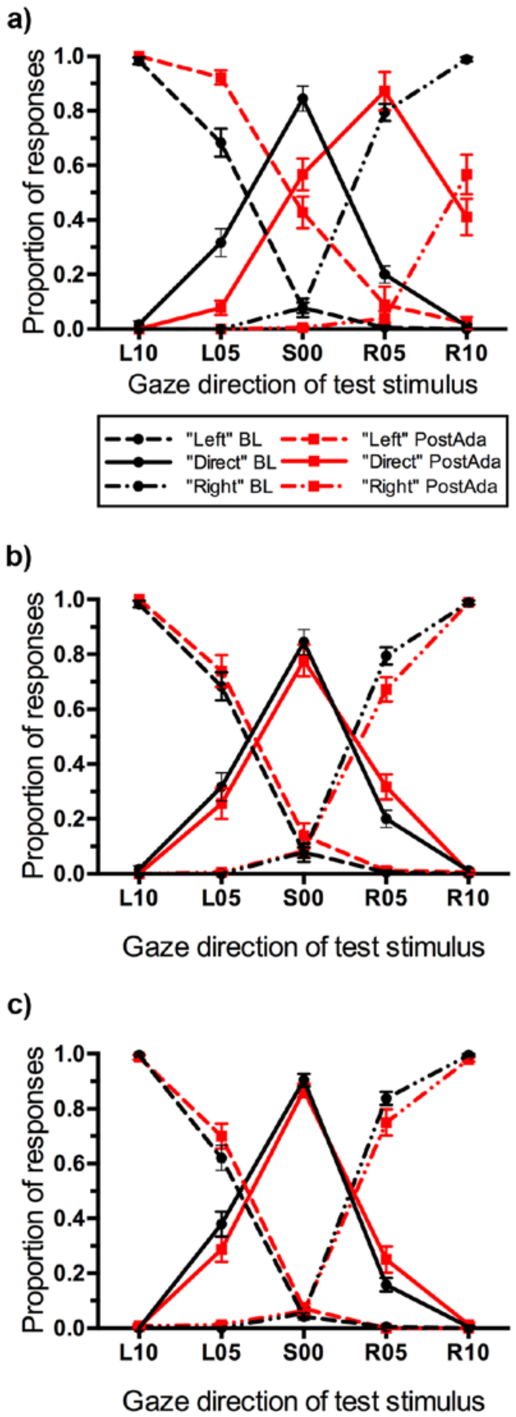

Figure 3. a) Immediate and b) long-term aftereffects for test stimuli with 5° and 10° rightward gaze observed in Experiment 1, c) long-term aftereffects for test stimuli with 5° and 10° rightward gaze observed in Experiment 2. Error bars indicate *SEM*s. * $p < .05$.