

The contributions of temporal delay and face exposure to the decay of gaze direction aftereffects

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Gaze direction is a dynamic social signal that provides real-time insight into another person's focus of attention. Gaze adaptation induces aftereffects in the perception of gaze in subsequent faces, typically biasing it away from the adapted direction. Previous studies found that such gaze direction aftereffects persist for about 7 min when repeatedly tested immediately after adaptation, but can survive at least 24 hr when there is no testing immediately after adaptation. These findings suggest that exposure to test faces after adaptation might affect the persistence of gaze direction aftereffects more than the passing of time. The present study systematically established the contributions of time and intervening testing on the longevity of gaze direction aftereffects. Aftereffects were induced and then traced over six postadaptation tests. Participants were assigned to four groups with a delay of either 30 s, 3 min, 5.5 min, or 8 min between adaptation and the first postadaptation test. Aftereffects were strongly affected by the number of preceding postadaptation tests, but unaffected by the delay between adaptation and test, revealing that face exposure affects the longevity of aftereffects more strongly than the passing of time, at least over the time frame studied here. Our findings suggest that exposure to a substantial number of faces with an unbiased distribution of gaze directions may be necessary to overcome gaze direction aftereffects.

Introduction

Gaze direction is an important social signal that can provide real-time insight into another person's mental state and focus of attention (Langton, Watt, & Bruce, 2000). Direct gaze creates eye contact, signals interest, and captures attention (von Grunau & Anston, 1995), whereas changes in someone's gaze direction can evoke reflexive attentional shifts in the observer (Driver et al., 1999; Friesen & Kingstone, 1998). The direction of gaze can also modify our perception of other social signals in the face, such as the attractiveness (Ewing, Rhodes, & Pellicano, 2010) and emotional expression of a person (Adams & Kleck, 2003, 2005; but see Bindemann, Burton, & Langton, 2008), and affect even very basic perceptual mechanisms underlying person identification (Kloth, Jeffery, & Rhodes, 2015) and the processing of face viewpoints (Bi, Su, Chen, & Fang, 2009). Underlining the social importance of gaze direction, it is assumed that accurate eye direction detection is an essential part of generating a theory of mind (Baron-Cohen, 1995).

Gaze direction perception is highly adaptable. Exposure to faces with a consistent gaze direction (e.g., strongly averted right gaze) induces shifts in the perceived gaze direction of subsequently presented faces in the opposite direction (e.g., to the left; Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006). Such *gaze direction aftereffects* are most obvious for faces with subtle gaze deviations in the adapted direction, which are typically less likely to be correctly

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classified than before adaptation, and instead tend to be falsely classified as looking straight ahead. Gaze direction aftereffects survive substantial changes in size and head orientation between adaptation and test stimuli (Jenkins et al., 2006) and have neural correlates in time windows from about 200 ms at occipito-temporal electrode sites (Kloth & Schweinberger, 2010; Schweinberger, Kloth, & Jenkins, 2007), indicating that they occur at high levels of visual processing. The magnitude of gaze direction aftereffects has been linked with participants' ability to correctly categorize gaze directions, which suggests a functional role of adaptation in gaze direction perception (Pellicano, Rhodes, & Calder, 2013).

Adaptation is not specific to gaze direction, but has also been shown to occur in the perception of other face signals, such as identity (Leopold, O'Toole, Vetter, & Blanz, 2001), emotional expression, sex, and ethnicity (Webster, Kaping, Mizokami, & Duhamel, 2004), as well as age (O'Neil, Mac, Rhodes, & Webster, 2014; Schweinberger et al., 2010; for a review, see Webster & MacLeod, 2011) and face viewpoint (Chen, Yang, Wang, & Fang, 2010; Fang & He, 2005; Jeffery, Rhodes, & Busey, 2006, 2007). It has been suggested that adaptation is functionally important, providing the face perception system with a mechanism to "self-calibrate," that is, to flexibly adjust neural response patterns of face-selective neurons to the characteristics of the specific subset of faces we experience. Down-regulation of neural responses to very frequent stimulus characteristics frees up resources to respond to different stimuli, likely enhancing the discrimination between similar stimuli and promoting novelty detection (Kohn, 2007; Ranganath & Rainer, 2003).

High-level aftereffects have many of the same temporal characteristics as low-level aftereffects, suggesting that they are closely related perceptual phenomena. Like low-level aftereffects, high-level face aftereffects increase logarithmically with increasing adaptation durations and decay exponentially as a function of the presentation duration of the test stimulus (Leopold, Rhodes, Muller, & Jeffery, 2005; Rhodes, Jeffery, Clifford, & Leopold, 2007). In the first study on the time course of the gaze direction aftereffect, Kloth and Schweinberger (2008) established the persistence of the aftereffect over several experimental phases. A gaze direction aftereffect was induced and quantified in a sequence of a pre-adaptation baseline phase, an adaptation block in which all presented faces displayed rightward gaze, and a postadaptation phase with top-up adaptors, in which test faces from the baseline phase were repeated, interleaved with top-up adaptor stimuli, to ensure high levels of adaptation were maintained throughout the postadaptation phase. Participants showed the well-established gaze direction aftereffect—that is, they were

dramatically less likely to correctly classify subtle rightward gaze after adaptation than before. The decay of this aftereffect was then tracked in a series of four postadaptation tests without top-up stimuli, separated by standardized 30-s breaks. Kloth and Schweinberger (2008) found that the aftereffect decayed exponentially, but remained significant until the third postadaptation test without top-ups, corresponding to about 7 min after the last adaptor had been presented (i.e., about 7 min after the end of the postadaptation phase with top-ups).

The fact that adaptation to a signal as dynamic as gaze direction led to aftereffects that persisted in the range of several minutes seemed remarkable. However, other recent evidence at the time suggested that other face aftereffects last much longer than that. Specifically, it was reported that face distortion aftereffects for famous faces could survive a full day (Carbon et al., 2007) or even a week (Carbon & Ditye, 2011), leading Kloth and Schweinberger (2008) to speculate that the time courses of aftereffects for different facial attributes might systematically vary, with adaptation to changeable face signals, like eye gaze direction, possibly leading to more short-lived aftereffects than adaptation to more invariant facial signals, like face distortions (cf. Haxby, Hoffman, & Gobbini, 2000).

More recent evidence, however, does not support this idea and instead suggests that the specific methodological details of adaptation paradigms might affect the persistence of aftereffects more strongly than the nature of the adapted signals. Kloth and Rhodes (2016) investigated the longevity of gaze direction aftereffects in a design similar to Carbon and colleagues' (Carbon & Ditye, 2011; Carbon et al., 2007), measuring aftereffects 24 hr after adaptation, either with only a single intervening postadaptation test on Day 1, or no intervening measurement of the aftereffect at all. Remarkably, they found small, but significant, gaze direction aftereffects 24 hr after adaptation in both cases. Considered in combination with the findings of Kloth and Schweinberger (2008), this result suggests that the longevity of gaze aftereffects depends to a large extent on the specific experimental procedure with which it is examined. In particular, the repeated testing of gaze direction discrimination performance after adaptation employed by Kloth and Schweinberger (2008) might have reduced the longevity of the aftereffect relative to its potential persistence when testing between adaptation and final test is minimized (Kloth & Rhodes, 2016). This conclusion is in line with a recent study that measured the decay of face identity aftereffects (over a short time period up until only 3000 ms after adaptation), which found that the aftereffect decayed with time, and that the presentation of intervening faces sped up this decline (Kiani, Davies-Thompson, & Barton, 2014).

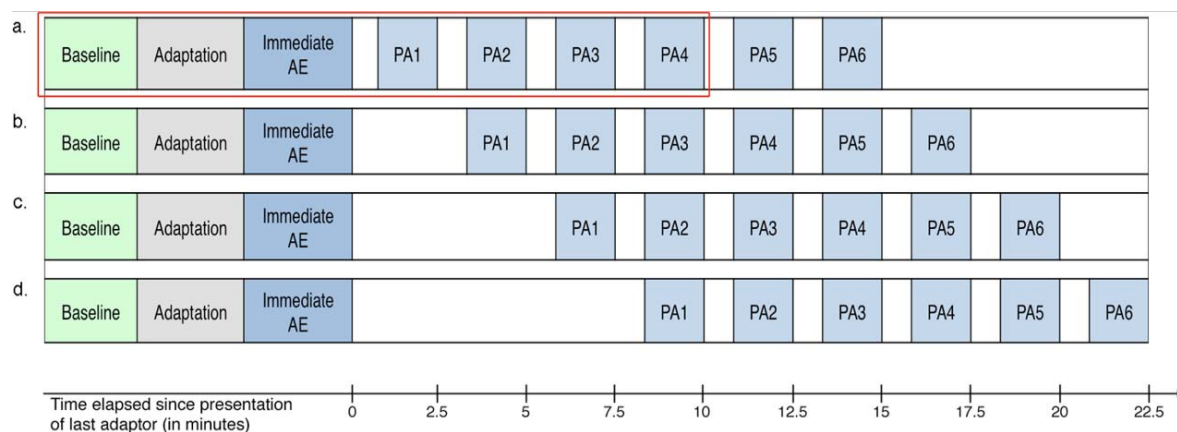


Figure 1. Overview of the general procedure of the experiment. The rows display the timing structure as experienced by participants in (a) the 30-s delay group, (b) the 3-min delay group, (c) the 5.5-min delay group, and (d) the 8-min delay group. The red frame indicates the timing structure employed by Kloth and Schweinberger (2008). AE = aftereffect, PA = postadaptation test.

In short, gaze direction aftereffects decay within minutes after adaptation when repeatedly tested, but can survive a whole day without any intervening testing (Kloth & Rhodes, 2016; Kloth & Schweinberger, 2008). However, compared to the magnitude of aftereffects tested immediately after adaptation, long-term (24-hr) gaze aftereffects are drastically reduced in magnitude (Kloth & Rhodes, 2016), suggesting that not only repeated exposure to test faces, but also the passing of time affect the decay of the aftereffect. To date, no study has systematically investigated the relative contributions of these two factors on the longevity of face aftereffects for a time window longer than 3000 ms after adaptation (Kiani et al., 2014, who studied the decay of identity aftereffects).

The present study was designed to close this gap and establish the effects of time elapsed since adaptation and the number of intervening test blocks on the persistence of gaze direction aftereffects. We employed a paradigm similar to Kloth and Schweinberger (2008). An initial sequence of a baseline phase, an adaptation block, and an immediate aftereffect test phase with top-up adaptors was used to induce and quantify a gaze direction aftereffect. The longevity of this aftereffect was then evaluated over six postadaptation phases without top-up adaptors. Critically, the temporal delay between the end of the immediate aftereffect test with top-up stimuli and the onset of the first postadaptation phase was varied between participants. The delay could either be 30 s (as in Kloth & Schweinberger, 2008), 3 min, 5.5 min, or 8 min (Figure 1). With these specific timing parameters, the first postadaptation phase for participants in the 8-min delay condition only started at a time at which participants in the 30-s delay condition had already completed three postadaptation phases and were not expected to show a significant gaze direction aftereffect any more (based on Kloth & Schweinberger, 2008). Based on the combined findings

of Kloth and Schweinberger (2008) and Kloth and Rhodes (2016), we predicted that the number of preceding postadaptation phases would strongly affect the persistence of the gaze direction aftereffect, but that the time since adaptation would have little, if any, effect on the presence of the aftereffect.

Methods

Participants

Eighty Caucasian adults took part in the study. Data from five participants were excluded from the analysis due to below-chance discrimination of rightward gaze during the baseline phase ($<33\%$ correct). The remaining 75 participants (25 men, 17–38 years, $M = 20 \pm 4$) reported normal or corrected-to-normal vision and were naive to the purposes of the study. Written informed consent was obtained from all participants before the experiment. Participants were debriefed after completing the study and received course credit for participation. The experimental procedure was in accordance with the ethical guidelines of the Declaration of Helsinki and approved by the Human Research Ethics Committee of the University of Western Australia.

Stimuli

The stimulus set consisted of photographs of six young male and six young female faces used in previous research (Calder, Jenkins, Cassel, & Clifford, 2008; Jenkins et al., 2006; Schweinberger et al., 2007). Each model posed at four different gaze directions. Pictures

of faces with 5° leftward, direct, and 5° rightward gaze were used as test stimuli. Pictures of faces with 25° rightward gaze were used as adaptor stimuli. Adaptor stimuli measured $6.4^\circ \times 10.4^\circ$. Test stimuli were presented at 75% the size of adaptors. A viewing distance of 52 cm was kept constant using a chin rest.

Task and procedure

Participants were randomly assigned to one of four groups, each with a different temporal delay between the end of adaptation and the first postadaptation test block. Participants in all four delay conditions underwent the same basic experimental sequence, consisting of a baseline phase, an adaptation block followed by an immediate aftereffect test in which test stimuli were interspersed with top-up adaptation stimuli, and a series of six more postadaptation tests without top-up adaptors that were equivalent to the baseline phase. Depending on the group participants had been assigned to, the temporal delay between the end of the immediate aftereffect test and the beginning of the first postadaptation test without top-up adaptors was either 30 s, 180 s (3 min), 330 s (5.5 min), or 480 s (8 min). The specific temporal staggering with a 150-s delay increase between groups was chosen because it corresponds to the duration of one postadaptation test and the following 30-s break, resulting in a design in which participants in the 8-min delay group started their first postadaptation test at exactly the same time as participants in the 5.5-min delay group started their second, participants in the 3-min delay group started their third, and participants in the 30-s delay group started their fourth postadaptation test (Figure 1).

Participants were instructed not to look at or interact with the experimenter during the delay period and did not see any other faces during this period. To keep them occupied during the delay period in a way that prevented them from being exposed to faces or pictures of faces, all participants, apart from those in the 30-s delay group, were given a simple word puzzle at the beginning of the testing session to work on during the waiting period. An acoustic signal 20 s before the beginning of the first postadaptation block indicated to go back into the chin rest and get ready for the next part of the experiment. Each postadaptation test block was separated from the subsequent test block by 30-s breaks during which a blank screen was presented. The timing of the sequence for the group of participants who had a 30-s delay between the immediate aftereffect test and the first postadaptation test was equivalent to that used by Kloth and Schweinberger (2008), the only difference being that two additional postadaptation phases were added to the procedure (Figure 1).

Baseline phase

The purpose of the baseline phase was to determine participants' general ability to accurately discriminate subtle differences in gaze direction. Thirty-six test faces (12 Identities \times 3 Gaze directions) were presented in random order. In each trial, a question mark was first presented (800 ms), was then replaced by the test face (400 ms), after which a blank screen was presented (2250 ms) during which participants responded (Figure 2a). Using the right index, middle, and ring fingers on three response keys, participants indicated for each face whether it looked to the left, straight ahead, or to the right. One baseline trial took 3450 ms, leading to an overall duration of the baseline phase of 2 min.

Adaptation block

Participants were presented with two consecutive runs of the 12 adaptation stimuli each, presented in randomized order. Adaptation stimuli displayed eye gaze averted 25° to the right and were presented for 3500 ms each, with an interstimulus interval of 200 ms (Figure 2b). The adaptation block had a total duration of about 1.5 min.

Immediate aftereffect test

The adaptation block was followed by the immediate aftereffect test. During this stage, the 36 test faces shown during the baseline phase were presented again (400 ms) in random order; however, this time each test face was preceded by two consecutive top-up adaptation faces (presented for 3500 ms each), to maintain maximal adaptation throughout the immediate aftereffect test. Top-up adaptors were passively viewed, and participants only responded to the test faces, which were preceded by question marks (1000 ms), indicating whether they perceived them to be looking to the left, straight ahead, or to the right (Figure 2c). To avoid potential effects of immediate repetitions of facial identities, neither of the top-up stimuli had the same identity as the following test face. An individual trial in the immediate aftereffect test took 10650 ms. The immediate aftereffect test therefore had a duration of about 6 min.

Postadaptation phase

After the variable delay separating the immediate aftereffect test from the first postadaptation test, a sequence of six postadaptation tests without top-up adaptation stimuli was run. These postadaptation tests were separated by 30-s breaks. The postadaptation tests were identical to the baseline phase, with the 36 test faces being presented again, for 400 ms each, in randomized order, and participants indicating the gaze

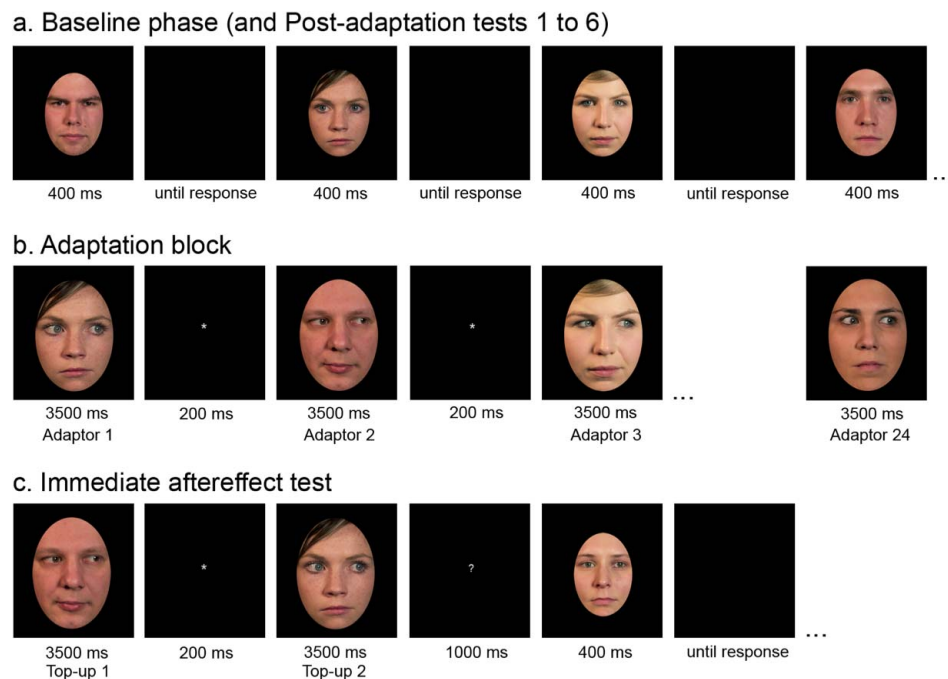


Figure 2. Trial procedure during (a) the baseline phase and the six postadaptation tests, (b) the adaptation block, and (c) during the immediate aftereffect test. For copyright reasons, the depicted identities are different from those used in the actual experiment.

direction of each face by button presses (Figure 2a). Each postadaptation test had a duration of about 2 min.

Results

Table 1 shows the proportions of left, direct, and right classifications for test faces with different gaze directions during baseline and the immediate aftereffect test. Adaptation to rightward gaze induced the

expected leftward shift in participants' perception of subsequently presented gaze directions. Most importantly, participants' ability to correctly classify rightward gaze dropped substantially (from 0.72 to 0.06), in favor of a drastic increase of incorrect direct classifications of rightward gaze (from 0.26 to 0.89).

For statistical analysis, aftereffect scores were calculated, for the immediate aftereffect phase and each of the six postadaptation phases, by subtracting the proportion of right responses made toward test faces with rightward gaze in each of the postadaptation phases from the proportion of right responses made

Gaze direction	Left gaze			Direct gaze			Right gaze		
Response	Left	Direct	Right	Left	Direct	Right	Left	Direct	Right
Baseline phase									
30-s delay	0.75 (0.14)	0.24 (0.12)	0.01 (0.06)	0.10 (0.10)	0.81 (0.12)	0.09 (0.07)	0.00 (0.00)	0.26 (0.18)	0.74 (0.18)
3-min delay	0.77 (0.16)	0.20 (0.15)	0.02 (0.05)	0.15 (0.13)	0.77 (0.16)	0.08 (0.08)	0.03 (0.05)	0.26 (0.12)	0.71 (0.14)
5.5-min delay	0.78 (0.18)	0.20 (0.16)	0.00 (0.00)	0.13 (0.13)	0.73 (0.23)	0.11 (0.15)	0.00 (0.00)	0.26 (0.21)	0.73 (0.21)
8-min delay	0.71 (0.18)	0.25 (0.14)	0.04 (0.10)	0.17 (0.16)	0.69 (0.16)	0.12 (0.10)	0.02 (0.04)	0.25 (0.17)	0.71 (0.21)
<i>M</i>	0.75 (0.17)	0.22 (0.14)	0.02 (0.06)	0.14 (0.13)	0.75 (0.17)	0.10 (0.10)	0.01 (0.03)	0.26 (0.17)	0.72 (0.18)
Immediate AE test									
30-s delay	0.89 (0.12)	0.09 (0.12)	0.00 (0.02)	0.35 (0.18)	0.63 (0.19)	0.00 (0.02)	0.02 (0.04)	0.90 (0.10)	0.07 (0.11)
3-min delay	0.95 (0.10)	0.05 (0.10)	0.00 (0.00)	0.42 (0.19)	0.57 (0.19)	0.01 (0.03)	0.07 (0.11)	0.89 (0.12)	0.04 (0.06)
5.5-min delay	0.89 (0.11)	0.11 (0.11)	0.00 (0.00)	0.28 (0.16)	0.71 (0.16)	0.00 (0.00)	0.02 (0.04)	0.93 (0.09)	0.05 (0.07)
8-min delay	0.93 (0.16)	0.04 (0.08)	0.02 (0.10)	0.39 (0.18)	0.56 (0.19)	0.03 (0.08)	0.06 (0.10)	0.84 (0.17)	0.09 (0.13)
<i>M</i>	0.92 (0.13)	0.07 (0.11)	0.01 (0.05)	0.36 (0.18)	0.62 (0.19)	0.01 (0.04)	0.04 (0.08)	0.89 (0.13)	0.06 (0.10)

Table 1. Mean proportions (and *SDs*) of left, direct, and right classifications for test faces with left, direct, and right gazes during the baseline phase and the immediate aftereffect test for participants in the four different delay groups. *Note:* AE = aftereffect.

towards rightward gazing faces during baseline. A positive aftereffect score indicates that adaptation decreased the accuracy of gaze direction perception for faces gazing in the adapted direction, with larger differences reflecting larger aftereffects. Data were analyzed in repeated-measures analyses of variance (ANOVA) as detailed in the subsections below. Where Mauchly's test indicated violations of the assumption of sphericity, degrees of freedom were corrected using the Greenhouse–Geisser procedure (when $\epsilon < 0.75$) or the Huynh–Feldt procedure (when $\epsilon > 0.75$; Field, 2009).

Immediate gaze direction aftereffect

Adaptation induced substantial immediate aftereffects for participants in each of the four delay groups ($M = 0.67$, $SD = 0.20$ in the 30-s delay group; $M = 0.68$, $SD = 0.15$, in the 3-min delay group; $M = 0.68$, $SD = 0.21$, in the 5.5-min delay group; and $M = 0.62$, $SD = 0.22$ in the 8-min delay group). To establish whether the immediate aftereffects observed in the different delay groups were of comparable magnitude, an initial one-way ANOVA was conducted on the immediate aftereffect scores for rightward gazing test stimuli, with delay group (30 s, 3 min, 5.5 min, 8 min) as a between-participants factor. There was no significant effect of delay group, $F(3, 71) = 0.33$, $p = 0.81$, $\eta_p^2 = 0.014$, indicating that the adaptation sequence induced initial aftereffects of comparable size in participants assigned to the different delay groups.

Factors affecting the longevity of the gaze direction aftereffect

To establish the contributions of the passing of time and exposure to test faces to the decay of the gaze direction aftereffect, aftereffect scores for the first to sixth postadaptation phase were entered into a repeated measures ANOVA with postadaptation phase (PA1, PA2, PA3, PA4, PA5, PA6) as a within-participants factor and delay group (30 s, 3 min, 5.5 min, 8 min) as a between-participants factor. The only significant effect was a main effect of postadaptation phase, $F(4.67, 331.81) = 28.60$, $p < 0.001$, $\eta_p^2 = 0.29$. There was no significant effect of delay group, $F(3, 71) = 0.16$, $p = 0.92$, $\eta_p^2 = 0.007$, and no significant interaction of postadaptation phase and delay group, $F(14.02, 331.81) = 1.20$, $p = 0.27$, $\eta_p^2 = 0.05$ (Figure 3).¹

To follow up on the main effect of postadaptation phase, aftereffect scores obtained for the different postadaptation phases were compared to zero to establish the longevity of the aftereffect. Aftereffects were found to be significantly larger than zero in the

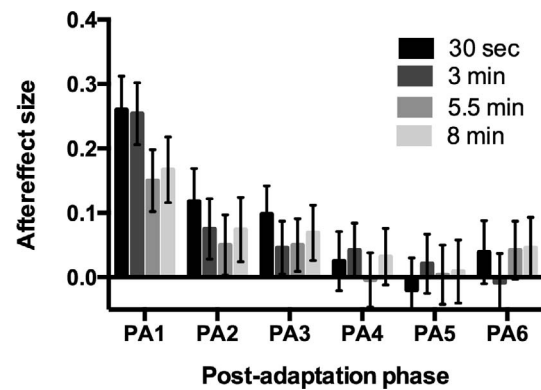


Figure 3. Gaze direction aftereffects in the six different postadaptation phases for each delay group. Error bars indicate SEMs.

first, $t(74) = 8.27$, $p < 0.001$, $d = 0.96$; second, $t(74) = 3.25$, $p = 0.002$, $d = 0.37$; and third postadaptation phase, $t(74) = 3.11$, $p = 0.003$, $d = 0.36$, but not in the fourth, $t(74) = 1.09$, $p = 0.28$, $d = 0.13$; fifth, $t(74) = 0.19$, $p = 0.85$, $d = 0.02$; and sixth postadaptation phase, $t(74) = 1.27$, $p = 0.21$, $d = 0.15$. These results indicate that the aftereffect lasted for about 7.5 min after adaptation for participants in the shortest delay group (cf. Kloth & Schweinberger, 2008) and for about 15 min after adaptation for participants in the longest delay group (Figure 1).

Discussion

We established the contributions of the time elapsed since adaptation and the number of intervening test phases on the decay of gaze direction aftereffects. Aftereffects were induced and then repeatedly tested over six postadaptation phases. The temporal delay between adaptation and the first postadaptation phase was varied between participants. The persistence of the aftereffect was found to be completely unaffected by this temporal delay. However, the number of previous test phases had a strong effect on whether the gaze direction aftereffect was still significant in a given test phase. The aftereffect lasted until the third postadaptation phase, which occurred 7.5 min after adaptation for participants in the shortest delay group and 15 min after adaptation for participants in the longest delay group.

Our study resolves an apparent discrepancy between previous findings on the longevity of gaze direction aftereffects. On the one hand, Kloth and Schweinberger (2008) found that aftereffects decay completely within about 7.5 min, using an experimental design in which aftereffects were tested immediately and repeatedly after adaptation. This finding was replicated here for

participants in the shortest delay group, for which the timing parameters of the experimental procedure were exactly the same as in Kloth and Schweinberger (2008). On the other hand, Kloth and Rhodes (2016) found that gaze direction aftereffects could survive a whole day, using an experimental design in which aftereffects were induced and then tested 24 hr later, with either only one or no test of the aftereffect immediately after adaptation. The combined results of these two studies suggested that the longevity of gaze direction aftereffects is very strongly affected by the frequency of intervening test phases, and less so by the sheer passing of time after adaptation. The results of the present study provide direct support for this interpretation, demonstrating that only the number of repeated tests, but not the time elapsed since adaptation, affect the persistence of gaze direction aftereffects, at least over the time window studied here.

Our results seemingly contradict those of Kiani et al. (2014), who found that identity aftereffects did decay with time (and that this decay was accelerated when another face was presented between adaptor and test). In light of the present results, their findings might indicate that face identity aftereffects are more sensitive to the temporal delay between adaptation and test than gaze direction aftereffects. However, it is likely that the drastically different temporal parameters between the two studies contributed to the different findings. Specifically, Kiani et al. induced face identity aftereffects on a trial-by-trial basis, exposing participants to a single adaptor for 5 s before measuring the aftereffect on a test face presented within 3000 ms after adaptation, either with or without the presentation of a single intervening face between adaptor and test. We, however, employed a blocked adaptation sequence in which participants adapted to rightward gaze for 1.5 min, followed by the immediate adaptation test in which each test stimulus was preceded by 7 s of top-up adaptation. It is plausible that this extended adaptation procedure would have induced larger and more persistent aftereffects than Kiani et al.'s procedure. Previous studies on low-level aftereffects have shown that even small increases in adaptation duration can drastically affect the persistence of aftereffects (Wolfe & O'Connell, 1986), suggesting that different adaptation durations might induce qualitatively different aftereffects, with shorter adaptation inducing only short-term fatigue and longer adaptation resulting in additional long-term structural changes that take longer to reset. It is plausible that aftereffects resulting from short-term fatigue might recover rapidly with time, whereas aftereffects resulting from more structural changes might be more long-lived and require exposure to an unbiased diet of gaze directions to reset.

Gaze aftereffects seem to play a functional role in gaze direction perception (Pellicano et al., 2013).

Adaptation calibrates the visual system by adjusting neural responses to the characteristics of current stimuli (Clifford, 2005; Webster, 2011), allowing for constancy in the response distribution across sensitive neurons despite changes in the distribution of stimuli (Benucci, Saleem, & Carandini, 2013; Gepshtein, Lesmes, & Albright, 2013; Ullman & Schechtman, 1982). In the context of the present study, the adaptation procedure presented the visual system with a strongly biased distribution of gaze directions, which led to the recalibration of neural responses across gaze-sensitive channels that resulted in the substantial behavioral aftereffect. Establishing the time course and longevity of gaze direction aftereffects is valuable because it can provide some insight into the principles that underlie the sampling of the distribution of gaze directions (e.g., over which time span or which number of faces does the visual system sample gaze directions?) and into the amount of time or unbiased gaze direction information that is necessary for the system to de-adapt completely (cf. Bao & Engel, 2012).

We have previously argued that evidence for gaze direction aftereffects that survive a whole day indicates sampling of prevailing gaze directions over extended time windows (i.e., gaze perception was still affected by exposure to a biased distribution of gaze directions 24 hr earlier), and we suggested that such sampling might be useful because it might yield more accurate estimates of the statistics (mean, range, etc.) of an input distribution than more time-restricted sampling (Kloth & Rhodes, 2016). However, the present findings suggest that the sampling of stimulus distributions is not predominantly time-locked, but instead depends on the frequency of face encounters. In the specific context of the present study, adaptation to a strongly biased sample of rightward gaze directions for about 2 min induced a substantial aftereffect that only reset after encountering three sets of 36 faces each that presented an unbiased sample of gaze directions, corresponding to about 6 min of de-adaptation. Importantly, it did not seem to matter whether those faces were encountered within only 7 or 15 min after adaptation. It is still plausible that such sampling over relatively large numbers of face encounters might provide more accurate estimates of the statistics of gaze directions than sampling over smaller numbers of faces.

It is an open question whether exposure to faces with an opposite bias in gaze direction might wipe out the aftereffect more quickly than faces with an unbiased diet of gaze direction. Moreover, it is yet unknown whether sheer exposure to faces with an unbiased distribution of the adapted signal is sufficient to reset gaze direction aftereffects (or any face aftereffect), or whether an active classification of the adapted signal is necessary for the decay to occur. An explicit gaze direction classification likely engages attention to gaze

more intensely than passive viewing. It has previously been shown that attention enhances face adaptation (Rhodes et al., 2011) and it seems likely that enhanced levels of task-induced attention to potentially de-adapting stimuli will also enhance recovery from adaptation. To empirically answer this question, future research might study the effects of intervening face presentations with and without the explicit task to classify the adapted signal, or with the task to classify an unrelated face signal, on the magnitude of gaze direction aftereffects.

In summary, we demonstrated that the longevity of gaze direction aftereffects depends strongly on the number of face presentations experienced after adaptation. In contrast, the passing of time after adaptation had no effect on the persistence of the aftereffect, at least over the time frame studied here. Irrespective of whether the first postadaptation test started only 30 s after adaptation or 8 min after adaptation, participants showed significant gaze direction aftereffects until the third postadaptation phase, at which time they had encountered more than 100 faces with an unbiased gaze direction distribution. Our findings therefore indicate that an extended sampling of unbiased gaze directions is necessary to overcome adaptation to a strongly biased distribution of gaze directions.

Keywords: face perception, face adaptation, gaze direction aftereffects, decay, time course

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Footnote

¹ Figure 3 suggests some effect of delay group, particularly in the first postadaptation phase. Upon reviewer recommendation, we therefore conducted an

additional univariate ANOVA to examine the effect of delay group separately for this phase. There was no significant effect of delay group, $F(3, 71) = 1.34$, $p = 0.27$, $\eta_p^2 = 0.05$. Equivalent univariate analyses for PA2 and PA3 showed that there was no significant effect of delay group in the second, $F(3, 71) = 0.32$, $p = 0.81$, $\eta_p^2 = 0.013$, and third postadaptation phases, $F(3, 71) = 0.31$, $p = 0.82$, $\eta_p^2 = 0.013$, either.

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