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The timecourse of higher-level face aftereffects

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Abstract

Perceptual aftereffects for simple visual attributes processed early in the cortical hierarchy increase logarithmically with adapting duration and decay exponentially with test duration. This classic timecourse has been reported recently for a face identity aftereffect [Leopold, D. A., Rhodes, G., Müller, K.-M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society of London, Series B, 272*, 897–904], suggesting that the dynamics of visual adaptation may be similar throughout the visual system. An alternative interpretation, however, is that the classic timecourse is a flow-on effect of adaptation of a low-level, retinotopic component of the face identity aftereffect. Here, we examined the timecourse of the higher-level (size-invariant) components of two face aftereffects, the face identity aftereffect and the figural face aftereffect. Both showed the classic pattern of logarithmic build-up and exponential decay. These results indicate that the classic timecourse of face aftereffects is not a flow-on effect of low-level retinotopic adaptation, and support the hypothesis that dynamics of visual adaptation are similar at higher and lower levels of the cortical visual hierarchy. They also reinforce the perceptual nature of face aftereffects, ruling out demand characteristics and other post-perceptual factors as plausible accounts.

Keywords: Visual perception; Face perception; Adaptation; Aftereffects

1. Introduction

Adaptive processes, which alter the operating characteristics of a system in response to changing inputs, are fundamental to sensory and perceptual coding (Clifford & Rhodes, 2005). By calibrating a limited neural response range to visual inputs, they can enhance discrimination (Abbonizio, Langley, & Clifford, 2002; Barlow, 1990; Clifford, Ma Wyatt, Arnold, Smith, & Wenderoth, 2001; Phinney, Bowd, & Patterson, 1997; Regan & Beverley, 1985; Watson, Rhodes, & Clifford, 2006; Werblin, 1973). By focussing neural responses on deviations from an adapted (average) state, they can result in neurally and computationally efficient coding (Leopold, Bondar, & Giese, 2006). By ensuring that people in shared visual environments have similar perceptual norms, they may produce a shared aesthetic experience such as the widespread preference for average exemplars (Rhodes, 2006; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Winkielman, Halberstadt, Fazendeiro, & Catty, 2006).

Visual adaptation can often bias perception away from the properties of adapting stimuli, towards opposite properties, resulting in perceptual aftereffects. Aftereffects have revealed much about the neural coding of simple visual attributes early in the cortical visual hierarchy (for reviews, see Clifford & Rhodes, 2005; Frisby, 1980). Aftereffects also occur for the perception of more complex stimuli, such as faces, and may therefore also be informative about higher-level cortical processing mechanisms. A variety of face aftereffects have been reported. For example, viewing a face produces an *identity aftereffect* in which perception is biased towards the opposite identity (Leopold, O'Toole,

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Vetter, & Blanz, 2001; Rhodes & Jeffery, 2006) and viewing consistently distorted faces produces a *figural aftereffect*, in which perception is biased towards the figurally opposite distortion (MacLin & Webster, 2001; Rhodes et al., 2003; Watson & Clifford, 2003; Webster & MacLin, 1999). Aftereffects also occur in the perception of eye gaze direction (Jenkins, Beaver, & Calder, 2006), gender, race and expression (Webster, Kaping, Mizokami, & Duhamel, 2004).

To explore the relationship between face aftereffects and traditional aftereffects with simpler visual attributes, Leopold, Rhodes, Müller, and Jeffery (2005) recently examined the temporal dynamics of the face identity aftereffect. They found that it increases logarithmically with adapting duration and decays exponentially with test duration, following the classic timecourse of aftereffects for many simple visual attributes, including tilt (Harris & Calvert, 1989; Magnussen & Johnsen, 1986; Wolfe, 1984), motion (Hershenson, 1989; Sekuler, 1975) and shape (Krauskopf, 1954). This result raises the intriguing possibility that the dynamics of adaptation are similar at higher and lower levels of the cortical visual hierarchy.

Alternatively, however, the classic timecourse of the identity aftereffect could be inherited from lower-level adaptation (cf. Kohn & Movshon, 2003). Leopold et al. (2005) did not eliminate such adaptation in their procedure, reasoning that face aftereffects are robust to changes in size or retinal position and primarily reflect adaptation of higher-level coding mechanisms.[1] However, although face aftereffects are not due *solely* to adaptation of low-level, retinotopic mechanisms, they may nevertheless have a retinotopic component, as indicated by reports that face aftereffects are reduced by changes in retinal position (e.g., Kovács, Zimmer, Harza, Antal, & Vidnyánszky, 2005; Yamashita, Hardy, De Valois, & Webster, 2005; Zhao & Chubb, 2001) and that distinct aftereffects can be generated for simultaneous adapting faces in distinct retinal locations (Afraz & Cavanagh, 2006).

The main aim of the present experiments was to determine whether face aftereffects still show the classic timecourse when low-level adaptation is eliminated using a size change between adapt and test face. To increase the generality of our results we examined two face aftereffects: the identity aftereffect and the figural face aftereffect. If we find the classic timecourse of logarithmic build-up and exponential decay then we would have evidence that the dynamics of adaptation are similar at higher and lower levels of visual processing. This timecourse would also highlight the perceptual nature of face aftereffects, and rule out demand characteristics or changes in post-perceptual decision processes. There are features of the figural aftereffect paradigm that may engage post-perceptual processes. After viewing obviously distorted test faces, participants must make subjective judgments of normality about (variously) distorted test faces. They might "decide" that faces with the adapting distortion "should" now be rated as most normal. This account would be ruled out if the figural aftereffect shows the classic timecourse.

[1] Retinotopic mechanisms could be adapted even though participants freely scanned the adapting faces, because fixations may favour certain features, e.g., the eyes (Yarbus, 1967).

2. Method

2.1. Participants

Seven adults (5 female) participated in the identity aftereffect task. Five (3 female) were naïve to the purpose of the study. Eight adults (5 female) participated in the figural aftereffect task. Six (4 female) were naïve to the purpose of the study. Five of the participants did both tasks, completing the identity task at least one month before the figural task.

2.2. Stimuli

2.2.1. Identity aftereffect

The stimuli consisted of an average male face (a morphed composite of 20 male faces) and four individual male faces together with their anti-faces (Face Set 2 from Leopold et al., 2005). The four individual faces were gray-scale photographs. An anti-face was created for each target face by morphing the structure of the average face away from the target by 80%. All the faces had the texture of the average face. The images were sharpened and placed inside an oval mask that hid most of the hair. Adapting faces subtended a visual angle of 13.0° horizontal and 16.7° vertical. The test face, which was always the average face, was smaller, subtending a visual angle of 5.9° horizontal and 8.4° vertical.

2.2.2. Figural aftereffect

The stimuli were gray-scale photographs of female faces. There were 12 adapting faces whose inner facial features had been distorted using the Photoshop Spherize function to a level of +50% (Expanded Adapt) or −50% (Contracted Adapt). These expand and contract distortions have been widely used to induce figural face aftereffects. There were four test faces, all of which were undistorted. Each participant saw only one of the four test faces. Adapting faces subtended a visual angle of 11.7° horizontal and 15.7° vertical. Test faces were smaller, subtending a visual angle of 6.0° horizontal and 8.3° vertical.

2.3. Procedure

2.3.1. Identity aftereffect

The procedure followed Leopold et al. (2005). Participants were first trained to discriminate the four identities (see Leopold et al., 2005 for details). The aftereffect was then measured using a rating task, in which participants rated their impression of the "identity strength" (for a cued identity) of a test face on a 7-point scale ranging from 1 = No Identity to 7 = Strong identity. "No Identity" meant that the test face had no distinguishing features of the cued identity. Because impressions could be dynamic, participants were asked to rate their impression at the offset of the test face.

Each trial consisted of a fixation cross (200 ms), a name cue X (1000 ms), an adapting face (variable duration), a test face (variable duration), a response screen displaying the question, "How strong was your impression of X?", where X was the cued name, and the rating scale. A warning beep sounded 250 ms before the end of the adapting face to alert participants to the upcoming test face. The adapting face was always an anti-face and the test face was always the average face. The next trial began 1000 ms after the participant responded. Five adaptation durations (1000, 2000, 4000, 8000, 16,000 ms) were crossed with 5 test durations (200, 400, 800, 1600, 3200 ms), with 12 trials in each combination (300 trials). Trials were divided into 15 blocks of 20, containing equal numbers of trials (4) at each adapting level and each test duration (but not fully crossed). Trials were randomised within blocks. The 15 blocks (300 trials) were completed in single session, which took around 1 h to complete.

2.3.2. Figural aftereffect

The figural aftereffect was assessed using ratings of perceived distortion. Each participant was assigned one of four different identities, which was used in the practice and test trials. They began by practicing rating subtle facial distortions in that face. Distortions were rated using a 7-point scale, ranging from 1 = Quite Contracted to 7 = Quite Expanded, with 4 representing "Normal" or undistorted. There were 42 practice trials, 6 at each of 7 distortion levels (−30, −20, −10, 0, 10, 20, 30). Each face was shown for 1000 ms and appeared immediately after the response to the previous one.

The adaptation trial sequence matched the identity aftereffect sequence, except that there was no fixation cross or name cue and the response screen asked, "How distorted did the face look?". The adapting face was either a contracted or expanded version of one of the 12 adapting identities. The test face was always the undistorted trained test identity. Each adapting identity (12) was shown once with each adapting distortion (contracted, expanded) at each adapting duration (1000, 2000, 4000, 8000, 16,000 ms) and each test duration (200, 400, 800, 1600, 3200 ms) (600 trials). Trials were divided into blocks of 40 trials (as for identity aftereffect) (20 for each distortion) and presented in random order. Participants completed 15 blocks of 40 (600 trials) over 2 sessions (8 blocks in first, 7 in second) of about 1 h each. Each session began with the distortion rating training.

3. Results

Following Leopold et al. (2005), the identity aftereffect was measured as the strength of impression of the test identity opposite the adapting identity. The figural aftereffect was measured as the difference in perceived distortion in the test face after adapting to contracted and expanded faces (perceived distortion after expanded adaptation minus perceived distortion after contracted adaptation). Given that the range over which the strength of impressions could vary for the figural aftereffect was half that of the identity aftereffect this measure ensures that the potential range of the two aftereffects is comparable. However, these are essentially non-commensurate scales, so we focus on the shape of the build-up and decay functions.

Both aftereffects showed the classic timecourse of a visual aftereffect, increasing with adapting duration and decreasing with test duration (Figs. 1 and 2). These effects were confirmed by separate ANOVAs conducted for each aftereffect, which both yielded large and significant effects of adapting and test duration (see Table 1).

The classic timecourses can also be seen in Fig. 3, where we plot the identity and figural aftereffects as a function of adapting duration (collapsed across test duration, Fig. 3a) and test duration (collapsed across adapting duration, Fig. 3b). Relative rating scores, in which each participant's overall mean has been subtracted from their scores, are used to facilitate comparisons between the two aftereffects. Both aftereffects increased monotonically with adapting duration (Fig. 3a) and decreased monotonically with test duration (Fig. 3b).

Timecourse data for the identity aftereffect with no size change (for the same stimuli), from Leopold et al. (2005), Face Set 2, are also shown on Fig. 3 (Identity-ProcB). The timecourse of this non-size-invariant identity aftereffect clearly matches that obtained here for the higher-level (size-invariant) component of the aftereffect (Identity-High). This match indicates that the classic timecourse obtained in the earlier study does not reflect adaptation of low-level components of the aftereffect.

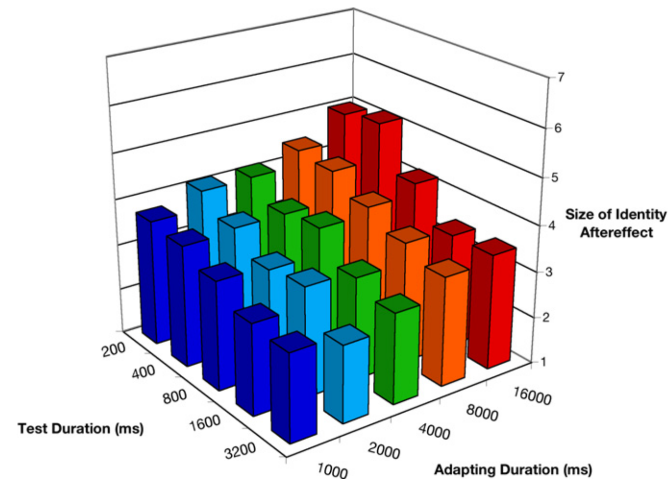

Fig. 1. Mean size of identity aftereffect as a function of adapting time and test duration ($N = 7$). Size of aftereffect was measured as the strength of impression of the cued identity (i.e., the identity opposite the adapting face).

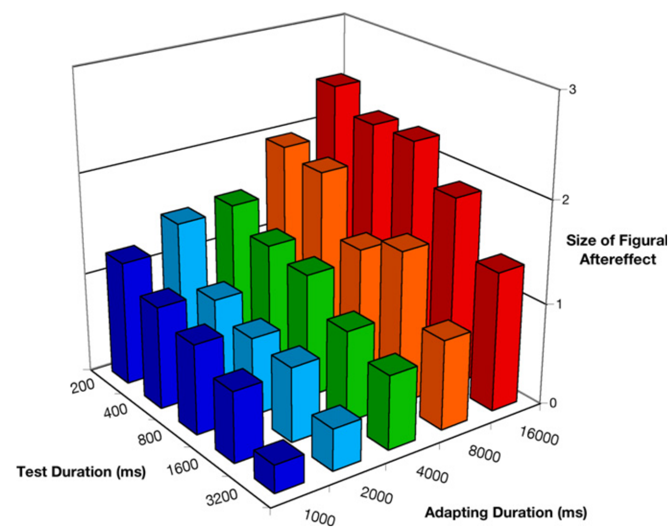

Fig. 2. Mean size of figural aftereffect as a function of adapting time and test duration ($N = 8$). Size of aftereffect was measured as the difference in distortion ratings following adaptation to expanded and contracted faces.

Table 1
Effects of adapting and test duration on the identity and figural aftereffects

	Identity aftereffect	Figural aftereffect
Effect of adapting duration	$F(4, 24) = 16.31$, $p < .0001$	$F(4, 28) = 34.87$, $p < .0001$
Effect of test duration	$F(4, 24) = 8.01$, $p < .0001$	$F(4, 28) = 7.83$, $p < .0011$
Interaction	$F(16, 96) = 2.20$, $p < .01$	$F(16, 112) = 0.66$, $p = .83$

Separate 2-way 5 × 5 ANOVAs were conducted for each aftereffect.

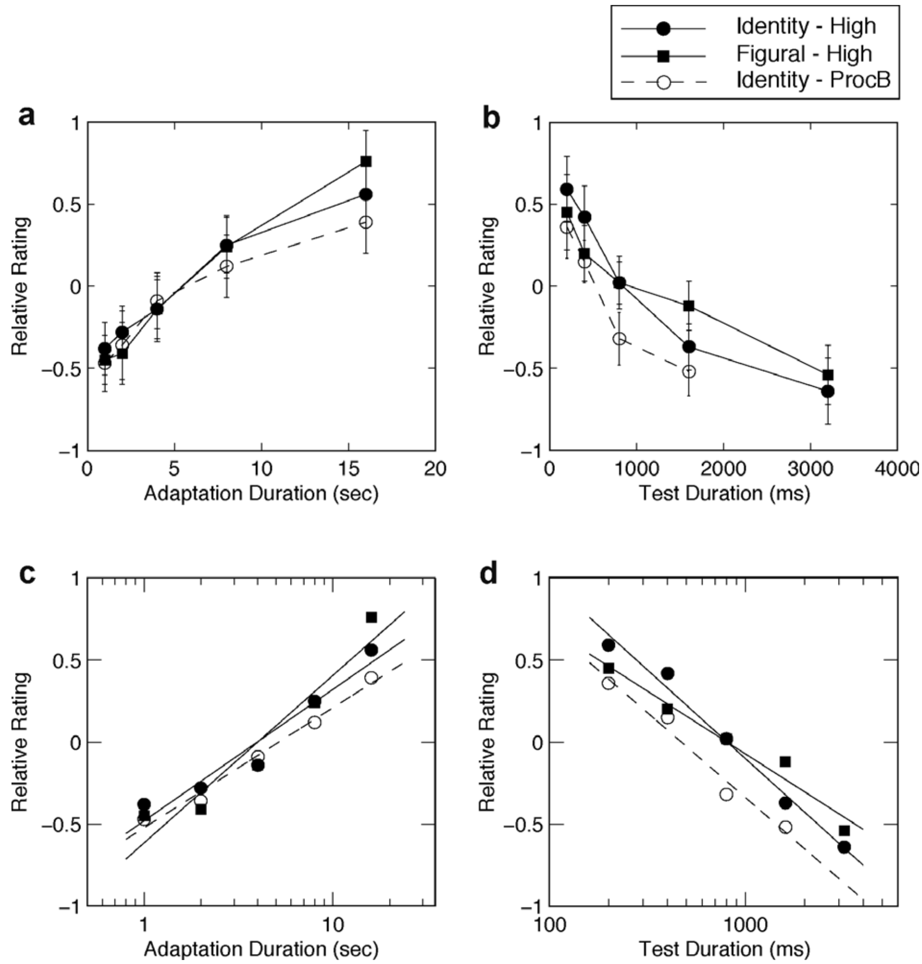

Fig. 3. Relative ratings (means ± SE) as a function of adapt and test duration for the high-level identity (Identity-High, $N = 7$) and figural (Figural-High, $N = 8$) aftereffects. Relative ratings for the non-size-invariant identity aftereffect (Identity-ProcB) ($N = 8$) for the same stimuli are also shown, replotted from Leopold et al. (2005). In these plots, each participant's grand mean was subtracted from their ratings to facilitate comparison of the timecourse of the aftereffects. (a) Relative ratings as a function of adapting time. (b) Relative ratings as a function of test duration. (c) Relative ratings plotted on semi-log co-ordinates, as a function of adapting time. (d) Relative ratings plotted on semi-log co-ordinates, as a function of test duration.

To further confirm that the higher-level identity and figural face aftereffects show the classic pattern of logarithmic build-up and exponential decay, the data are re-plotted on semi-log co-ordinates in Fig. 3c and d, where they should appear as straight lines. Straight line fits to the group data were excellent with R^2 values of .94 and .99 for the adapt and test functions, respectively, of the high-level identity aftereffect, and .92 and .96 for the adapting and test functions, respectively, for the high-level figural aftereffect. Again, the timecourse data for the high-level identity aftereffect (Identity-High) matches that obtained without a size change (Identity-ProcB). Fits for the latter were also very high ($R^2 = .98$ and .97 for the adapt and test functions, respectively). Moreover, very similar slopes were observed for the two identity aftereffects, for both the adapting (0.80 ± 0.09, Identity-High; 0.73 ± 0.08, Identity-ProcB) and test (-1.07 ± 0.16, Identity-High; -1.03 ± 0.14, Identity-ProcB) duration functions, $F(1, 66) = 0.29$, $p = .59$ (adapt duration) and $F(1, 59) = 0.03$, $p = .86$ (test duration). Runs tests indicated no significant non-linearities (all p's > .50).[2]

4. Discussion

Both the face identity aftereffect and the figural face aftereffect exhibited the classic timecourse of logarithmic build-up and exponential decay, seen for traditional perceptual aftereffects with simpler visual attributes. This timecourse cannot be a flow-on effect of low-level retinotopic adaptation, which was eliminated by using different sized adapt and test faces. Rather it suggests that the dynamics of higher-level adaptation may be similar to those of lower-level adaptation. This similarity may reflect physiological constraints imposed by the cellular (e.g.,

[2] We cannot compare the slopes of the identity and figural aftereffects because these are measured on different scales and the slopes are not scale-invariant (doubling scale values will double the slope).

hyperpolarization) and network mechanisms (e.g., changes in inhibition and relative activation of competing groups of neurons) that underlie adaptation (see Ibbotson, 2005 for a review). In other words, local dynamics among neurons at different cortical processing stages might similarly shape aftereffects for diverse stimuli.

The face aftereffects studied here may well reflect adaptation in high-level face-coding areas, such as the FFA and OFA, which code individual facial structure (Gauthier et al., 2000; Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher & Yovel, 2006). FFA activity is also associated with our perceptual experience of faces (George et al., 1999; Rotshtein, Henson, Treves, Driver, & Dolan, 2005) and is sensitive to deviations from the average face (Loffler, Yourganov, Wilkinson, & Wilson, 2005), which is needed for the aftereffects examined here. It is possible that non-face-selective mechanisms, such as mid-level shape coding mechanisms (Suzuki, 2005), also contribute. The general point would still stand, however, that the dynamics of adaptation for post-retinotopic coding mechanisms (for mid-level shape and/or faces) resemble those of low-level, retinotopic coding mechanisms.

The classic timecourse for identity and figural face aftereffects also reinforces their perceptual nature and rules out demand characteristics and other post-perceptual factors as plausible accounts. It will be interesting to determine whether other face aftereffects, such as viewpoint, gender, race and expression aftereffects also show the classic timecourse. Preliminary evidence that face viewpoint aftereffects are sensitive to adapting duration (bigger for 5 s than 200 ms of adaptation) suggests that they might (Fang & He, 2005). Expression aftereffects also appear to be sensitive to adapting duration, occurring after 5000 ms, but not 500 ms, of adaptation (Hsu & Young, 2004). Nothing is known about the timecourse of changes in the perceived boundaries of gender and race categories induced by adaptation (Webster et al., 2004).

Our results demonstrate that face aftereffects can be induced with much shorter adaptation times than previously supposed. Figural face aftereffects are typically induced with several minutes of adaptation, but were obtained here with as little as one second of adaptation (with brief test stimuli). Five seconds was thought to be the lower limit for inducing identity aftereffects (Leopold et al., 2001), but with the face-verification procedure used here, aftereffects were seen at shorter adapting durations. Our finding that robust face aftereffects can be generated with brief adapting durations is an important methodological contribution, which should result in more efficient designs for face adaptation studies.

Finally, we found some evidence that stronger face aftereffects decay more slowly than weaker ones, as indicated by the significant interaction between adapt and test duration for the identity aftereffect (see also Fig. 1). A similar effect has been observed for aftereffects with simpler stimuli (e.g., linear motion, Hershenson, 1989). However, the interaction did not occur for either the figural face aftereffect (Fig. 2) or the identity aftereffect without a size change (Leopold et al., 2005), suggesting that it may not be a robust effect, at least over the adapting durations used here.

Adaptive coding mechanisms are fundamental to perceptual analysis. Our results suggest that they may operate in the same way, regardless of what information is being coded or where in the cortical visual hierarchy adaptation is occurring. This similarity could occur because networks at different cortical processing stages have similar temporal dynamics, as suggested above. However, given that any visual experience is a result of activity throughout the visual system, the dynamics could alternatively be a property of this global activation. Imaging and neurophysiological studies that relate activation in different visual areas to the experience of face aftereffects should help reveal the source of these dynamics. It seems likely that higher-level, face coding areas such as the FFA and OFA, will be involved, although earlier cortical areas, particularly mid-level shape coding areas, may also contribute.

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