Electrophysiological correlates of eye gaze adaptation

Nadine Kloth  
Department of Psychology, University of Jena, Germany

Stefan R. Schweinberger  
Department of Psychology, University of Jena, Germany

Recent research shows a strong effect of adaptation on gaze perception: Adaptation to faces with eye gaze constantly diverted in one direction subsequently impairs the perception of that gaze direction. A previous study on the neural correlates of this effect found that N170 amplitudes to test faces were strongly attenuated following adaptation. ERP modulations as a function of gaze direction adaptation, however, were found only later (250–350 ms). Here, we used a new paradigm to study the exact nature of both the gaze direction-invariant N170 attenuation effect and the direction-specific effects in later time windows. We compared the ability to classify gaze direction before and after adaptation to direct gaze (control condition) or to eye gaze diverted to the right (adaptation condition). Behavioral results clearly replicated earlier findings of an impaired perception of eye gaze directed to the adapted side. The ERP analysis confirmed an insensitivity of the N170 to gaze adaptation, suggesting that reported attenuations resulted from adaptation to generic face information irrespective of gaze direction. Occipitotemporal ERPs ~250–350 ms showed direction-specific modulations with most positive amplitudes in response to stimuli gazing in the direction of adaptation. Finally, there was an effect in the parietal late positive component ~400–600 ms, which we interpret as a neural correlate of adaptation-induced novelty detection.

Keywords: ERP, face perception, gaze perception, high-level adaptation, N170, P3


Introduction

The systematic application of adaptation paradigms has a long tradition in vision research. For literally hundreds of years, perceptual aftereffects have been reported and studied for the early stages of visual processing and for relatively simple stimulus characteristics such as luminance, contrast (Chen, Zhou, Gong, & Liang, 2005), color, or motion (Antal et al., 2004). One of the most famous examples is the motion aftereffect (MAE) in which the prolonged viewing of a unidirectionally moving stimulus subsequently leads to the illusory perception of motion in opposite direction in a static image (Purkinje, 1820, see Anstis, Verstraten, & Mather, 1998, for a review). This phenomenon has been attributed to a disequilibrium between motion detectors selectively tuned to opposite directions; and the systematic investigation of the MAE, as one example of perceptual aftereffects, has therefore offered detailed insight into the organization of the neural system processing motion direction—with distinct subsystems detecting motion in opposite directions.

A striking discovery within the past decade was that adaptation is also of central importance for the perception of very complex visual stimuli, such as human faces. Webster and MacLin (1999) reported the face distortion aftereffect (FDAE), a figural aftereffect in the perception of face configurations. They found that adaptation to distorted (e.g., contracted) faces subsequently led to an altered perception of normal faces as being distorted in the direction opposite to adaptation (e.g., expanded). Similar high-level contrastive aftereffects have also been reported for other face-related processes such as the perception of identity (Leopold, O’Toole, Vetter, & Blanz, 2001), gender (Kovács et al., 2006), viewpoint (Fang, Ijichi, & He, 2007), ethnicity and emotional expression (Webster, Kaping, Mizokami, & Duhamel, 2004), and eye gaze direction (Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006). Jenkins et al. (2006) found that adaptation to a certain eye gaze direction dramatically impaired participants’ subsequent ability to perceive eye gaze in that direction. They presented participants with a series of faces with gaze universally directed 25° to either the left or right side. Following adaptation, participants typically perceived smaller gaze deviations into the adapted direction as looking directly at them. This effect was found to be symmetric, i.e., the influence of adaptation on the perception of gaze into the adapted direction was equivalent for left and right adaptation directions.

Importantly, in showing that these effects are to a large extent size- and position invariant, the interpretation that complex figural aftereffects might merely reflect adaptation to low-level characteristics of the stimuli has been carefully ruled out. At the same time, it has been shown that high-level aftereffects share some characteristics with low-level aftereffects, especially with regard to their time course, which has been described as following a logarithmic buildup (Leopold, Rhodes, Müller, & Jeffery, 2005) and an exponential decay (Kloth & Schweinberger, 2008).

As has earlier been demonstrated for lower levels of the visual hierarchy, the examination of aftereffects in face perception also allows a deeper insight into the functional
organization of the mechanisms underlying face perception (see Calder, Jenkins, Cassel, & Clifford, 2008, for a study applying gaze adaptation to investigate the nature of gaze direction coding). Unsurprisingly, the investigation of face aftereffects received much recent attention, and an increasing number of studies use adaptation paradigms to improve our understanding of the processes underlying face perception. The putative mechanisms of aftereffects are almost universally described in terms of neural coding (Grill-Spector, Henson, & Martin, 2006). Accordingly, the neural bases of face aftereffects have been investigated using neuroimaging (e.g., Fang, Murray, & He, 2007; Grill-Spector et al., 2006; Kovács, Cziraki, Vidnyánszky, Schweinberger, & Greenlee, 2008; Löffler, Yourganov, Wilkinson, & Wilson, 2005; Mazard, Schiltz, & Rossion, 2006) or electrophysiological methods (Kloth, Schweinberger, & Kovács, 2010; Kovács et al., 2006; Kovács, Zimmer, Harza, Antal, & Vidnyánszky, 2005; Kovács, Zimmer, Harza, & Vidnyánszky, 2007). By contrast, the specific phenomenon of eye gaze adaptation is a relatively recent discovery, and only few studies so far investigated neural correlates of these aftereffects (Calder et al., 2007; Schweinberger, Kloth, & Jenkins, 2007).

In the only prior electrophysiological study on eye gaze adaptation, we investigated modulations of the event-related potentials (ERPs, Schweinberger et al., 2007). Participants classified the gaze direction of test faces before and after adaptation to faces with eye gaze directed to one constant direction (with separate blocks of left and right gaze adaptation, respectively). Importantly, test stimuli in post-adaptation trials were always immediately preceded by top-up adaptation displays in order to ensure a maximal level of adaptation throughout (cf. Jenkins et al., 2006, see also Seyama & Nagayama, 2006). The results closely replicated those by Jenkins et al. (2006) in showing that adaptation strongly biased participants to classify gaze in the adapted direction as “direct.” The analysis of the ERPs evoked by test stimuli revealed a substantial N170 amplitude reduction (and latency increase) in response to test faces in post-adaptation trials as compared to test faces before adaptation. Strikingly, this N170 attenuation was independent of the direction of prior adaptation (i.e., left vs. right), which may be surprising considering that the N170 component has been proposed to be strongly driven by the eye region of a face (Itier, Latinus, & Taylor, 2006; Schyns, Jentzsch, Johnson, Schweinberger, & Gosselin, 2003). In our study, however, direction-specific effects were found not earlier than ~250–350 ms.

Given the direction invariance of the N170 attenuation, we had speculated that it reflected adaptation to more general face-related information (such as the structural composition of faces) independent of eye gaze direction. This is in line with the idea of the N170 as predominantly reflecting the processing of structural (or configurual) face information in upright faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Kanwisher & Moscovitch, 2000; Rossion et al., 2000). Moreover, since the publication of our previous paper (Schweinberger et al., 2007), strong and systematic effects of categorical face adaptation have been detected on both the N170 (Kloth et al., 2010; Maurer, Rossion, & McCandliss, 2008), and its neuro-magnetic equivalent, the M170 (Harris & Nakayama, 2007). In short, this brain response ~170 ms is strongly attenuated for a face when immediately preceded by another face, and is much larger when a face was either preceded by a stimulus from a different object category, or when separated from a previous face by a larger time interval. Consequently, a pre-adaptation baseline, while common and suitable in behavioral research on face aftereffects, is unsuitable for the investigation of ERP correlates of adaptation to specific aspects of facial information (such as gaze direction, gender, etc.). To avoid any confound between categorical face aftereffects and directional gaze aftereffects in the context of the present ERP study, we modified our previous adaptation paradigm in a way that allowed comparing effects of adaptation to a certain gaze direction (i.e., adaptation to right gaze) with a direction-neutral adaptation condition that replaced the control (pre-adaptation) condition used in Schweinberger et al. (2007). We reasoned that faces displaying direct gaze would best fulfill the criteria of both preserved categorical face information and horizontally non-directional gaze. Thus, general face information preceding a test face was equivalent for control and directional post-adaptation phases.

On the basis of earlier findings (cf. Jenkins et al., 2006; Schweinberger et al., 2007; Seyama & Nagayama, 2006), we reasoned that direct gaze adaptation should elicit similar behavioral effects as a classical pre-adaptation baseline (but see Calder et al., 2008). Similarly, justified by findings demonstrating symmetrical aftereffects for right and left gaze adaptation (Jenkins et al., 2006; Schweinberger et al., 2007; Seyama & Nagayama, 2006), and to avoid carryover effects due to temporal persistence of opposite gaze aftereffects (Kloth & Schweinberger, 2008), we decided to use only one (right) directional adaptation condition. Given the equivalent amount of face exposure preceding test faces in the control and directional adaptation condition, we did not expect an N170 attenuation for right gaze-adapted trials relative to direct gaze-adapted trials. Rather, we expected direction-specific aftereffects not earlier than ~250 ms after stimulus onset (cf. Schweinberger et al., 2007). Finally, recent studies on neural correlates of perceptual adaptation to gender revealed that a centroparietal late positive component (LPC, ~400–600 ms) was increased as a function of the physical difference on the classification dimension (in that case, masculinity–femininity) between adaptor and test stimuli. Intriguingly, these findings were obtained following adaptation to both face (Kloth et al., 2010) and voice gender (Zäske, Schweinberger, Kaufmann, & Kawahara, 2009). The LPC effect may well represent a more general neural correlate of adaptation-induced novelty detection. Specifically, it is assumed that adaptation...
improves the discriminability of novel stimuli by decreasing response magnitude to more frequent (less deviant) stimuli, thereby increasing response magnitude to deviant stimuli. Based on this assumption, we predicted an analogous relationship between LPC amplitude and adaptor–test dissimilarity in the present experiment on gaze adaptation, and we therefore analyzed LPC amplitudes, in addition to earlier ERPs.

Methods

Participants

Twenty naive participants (20 to 28 years, M = 22.7 years, 10 men), who were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), contributed data and received course credit or payment for their participation. They all reported normal or corrected-to-normal vision and gave their informed consent prior to data acquisition.

Stimuli

Test faces were color photographs of 6 male and 6 female young adults. Each model posed at five gaze angles: 10° left (L10), 5° left (L05), direct (S00), 5° right (R05), and 10° right (R10; all directions from the observer’s point of view). A subset of these stimuli also served as adaptation stimuli. The stimuli showing direct gaze (S00) served as control (direct) adaptors and the stimuli showing 10° gaze deviation to the right (R10) served as right adaptors.

Test faces (8.0 × 14.0 cm) were presented at a viewing distance of ~87 cm, which was kept constant by using a chin rest. Adaptation stimuli were presented at 150° the size of test stimuli so that the eye regions in adaptation and test stimuli were non-overlapping.

Apparatus

The electroencephalogram (EEG) was recorded from 32 Ag/AgCl electrodes (AC, 0.05–40 Hz, 250 Hz sampling rate) at locations Fz, Cz, Pz, Iz, Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10, PO9, and PO10, with TP10 as initial common reference, using an Easy-Cap. Electrode impedances were kept below 10 kΩ. The horizontal electrooculogram (EOG) was recorded from the outer canthi of both eyes, and the vertical EOG was monitored bipolarly from above and below the right eye. Offline, data were segmented into epochs of 2200 ms (200 ms prestimulus baseline) and trials were inspected for ocular (e.g., blinks, saccades) and non-ocular artifacts. Trials with non-ocular artifacts were discarded. For all other trials, the EEG was corrected for contributions of vertical and horizontal eye movements using BESAs automatic EOG artifact correction based on an adaptive artifact correction (Ille, Berg, & Scherg, 2002). Data were digitally low-pass filtered at 20 Hz (zero phase shift, 12 dB/oct) and recalculated to average reference.

Procedure

The experiment began with a conventional pre-adaptation test, which was announced as a block of practice trials. The pre-adaptation test closely followed the classical one as applied by Jenkins et al. (2006) and in our earlier study (Schweinberger et al., 2007). The results allowed determining participants’ baseline ability to identify eye gaze direction without any prior adaptation. Using right index, middle, and ring fingers on three response keys, participants indicated whether a test face showed left, direct, or right gaze direction. Altogether, the pre-adaptation test consisted of 72 test faces, with each of the twelve identities presented once in each of the L10, L05, R05, and L10 conditions and twice in the S00 condition. For each trial, a question mark was first presented (800 ms), was then replaced by the test face (400 ms), followed by a blank screen (2250 ms) during which participants responded (see Figure 1). The implementation of this pre-adaptation test aimed at comparing its results to the behavioral data recorded in the new control condition—the direct gaze adaptation condition—therefore allowing the examination of possible effects of adaptation to direct gaze. During this stage of the experiment, no EEG was recorded.

The major experiment consisted of two main blocks: one block investigated the effect of adaptation to direct eye gaze, the other block examined the effect of adaptation to right eye gaze direction—with block order counterbalanced across participants. At the beginning of each adaptation phase, twelve adaptation stimuli with gaze constantly directed in the direction of adaptation were presented twice in randomized order. Exposure duration was 3500 ms each with an inter-stimulus interval of 200 ms. For each of the two blocks, the adaptation sequence was immediately followed by a post-adaptation test with 216 test trials. To maintain a high level of adaptation throughout the post-adaptation test, the blocked presentation of adaptation stimuli was repeated after 108 test trials. After each series of 54 post-adaptation test trials, the experiment was interrupted for a self-paced break, to ensure that the EEG remained relatively uncontaminated by artifacts such as blinks, eye movements, or excessive alpha activity, which may occur as a result of fatigue. The test trials consisted of 36 presentations (12 identities × 3 repetitions) of L10, L05, R05, and R10 stimuli, respectively, and of 72 presentations (12 identities × 6 repetitions) of S00 stimuli. The presentation of an equal number of test stimuli gazing in the left direction (L10, L05), right direction (R10, R05), and directly at the observer (S00)

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aimed at requiring an equal amount of “left,” “right,” and “direct” responses, therefore discouraging any response bias. Post-adaptation trials began with the presentation of a so-called “top-up” adaptation display (3500 ms), which was an adaptor stimulus serving the purpose of maintaining a high level of adaptation throughout the whole post-adaptation block. Top-up adaptors never carried the same identity as the subsequently presented test face. The top-up adaptor was followed by the presentation of a question mark (1000 ms), the test stimulus (400 ms), and a blank screen during which participants responded (2250 ms). For an overview of the procedure, see Figure 1.

**Results**

**Behavioral results**

Data were analyzed using repeated measures analyses of variance (ANOVA). Where appropriate, epsilon corrections for heterogeneity of covariances were performed (Huynh & Feldt, 1976). Unless otherwise stated, all post-
hoc \(t\)-tests were corrected according to the Bonferroni procedure. At first, the patterns of "direct" classifications obtained in the pre-adaptation test (no adaptation condition) and in the control condition (direct adaptation condition) were analyzed (see Table 1 and Figure 2).

An ANOVA with the factors Adaptation (no, direct) and Direction of gaze in test faces (L10, L05, S00, R05, and R10) revealed only a main effect of Direction \((F[4, 76] = 258.22, p < 0.001)\), which had to be expected, but no main effect of Adaptation \((F[1, 19] < 1)\) and no interaction of Adaptation and Direction \((F[4, 76] < 1)\). This finding indicates that adaptation to direct gaze did not lead to any aftereffects, and that the direct gaze adaptation condition can therefore serve as a neutral control condition for the main experiment (see also Figure 2).

In a second step, the behavioral results of the main experiment were analyzed in an ANOVA with Adaptation (direct, right) and Direction of gaze in test faces (L10, L05, S00, R05, and R10) as factors. This analysis revealed significant main effects of Adaptation \((F[1, 19] = 8.32, p < 0.05)\) and Direction \((F[4, 76] = 187.54, p < 0.001)\), as well as an interaction of these factors \((F[4, 76] = 39.90, p < 0.001)\). Planned comparisons confirmed that adaptation to right gaze (as compared to direct gaze) led to a significant increase of incorrect "direct" classifications of test stimuli gazing 5° to the right (64.17% vs. 33.47%; \(t[19] = 7.72, p < 0.001\)) and 10° to the right (13.33% vs. 5.97%; \(t[19] = 3.58, p < 0.01\)). Adaptation to right gaze further led to a significant decrease of incorrect "direct" classifications of faces gazing 5° to the left (20.00% vs. 28.33%; \(t[19] = 2.47, p < 0.05\)). Finally, there was a trend for a smaller number of correct classifications of direct gazing test stimuli following right as compared to direct adaptation (84.58% vs. 89.65%; \(t[19] = 1.98, p = 0.062\)). For an overview of the results, see Table 1 and Figure 2.

### Electrophysiological results

Following direct gaze adaptation, the mean numbers of artifact-free trials contributing to the individual averaged ERP were 34.9, 34.8, 34.8, 34.9, and 70.2 for L05, R05,
L10, R10, and S00 test stimuli, respectively. After right gaze adaptation, the L05, R05, L10, R10, and S00 conditions were represented by 35.1, 35.6, 35.2, 35.4, and 70.4 trials, respectively. In analogy to the analysis of behavioral results, epsilon corrections for heterogeneity of covariances were performed when appropriate (Huynh & Feldt, 1976). Unless stated otherwise, all post-hoc $t$-tests were corrected according to the Bonferroni procedure ($\alpha = 0.05$).

**P1**

A repeated measures ANOVA on Electrode site (O1/O2, TP9/TP10, P9/P10, and PO9/PO10), Laterality (left, right), Adaptation condition (direct, right), and Direction of gaze in test faces (L10, L05, S00, R05, and R10) revealed a main effect of Electrode site ($F[3, 57] = 44.84, p < 0.001$), reflecting the typical occipital P1 topography, and a main effect of Adaptation condition ($F[1, 19] =$

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**Figure 3.** Grand average ERPs over 20 participants evoked by test faces gazing in the (top) left direction or (bottom) directly at the observer depending on whether participants had earlier adapted to direct gaze (black) or to gaze directed to the right (red).
7.42, \( p < 0.05 \), reflecting small but significant P1 amplitude differences between trials following direct gaze adaptation (\( M = 3.06 \mu V \)) and right gaze adaptation (\( M = 2.90 \mu V \)).

The analysis of P1 latencies at electrodes O1 and O2 revealed no significant effects (all \( ps > 0.10 \)).

N170

Figure 3 depicts ERPs following adaptation to direct and right gazes for test faces with all five gaze directions at selected electrode locations. Visual inspection did not suggest clear adaptation effects on N170 amplitudes. This was confirmed by an ANOVA on Electrode site (P7/P8, TP9/TP10, P9/P10, and PO9/PO10), Laterality (left, right), Adaptation condition (direct, right), and Direction of gaze in test faces (L10, L05, S00, R05, and R10), which revealed only a significant main effect of electrode site (\( F[3, 57] = 12.57, p < 0.001 \)), reflecting the typical occipitotemporal N170 topography. Similarly, the analysis of N170 peak latencies revealed no significant effects (all \( ps > 0.10 \)).

250–350 ms

An ANOVA with the factors Electrode site (P7/P8, TP9/TP10, P9/P10, and PO9/PO10), Laterality (left, right), Adaptation condition (direct, right), and Direction of gaze in test faces (L10, L05, S00, R05, and R10) revealed main effects of Electrode site (\( F[3, 57] = 36.72, p < 0.001 \)) and Direction (\( F[4, 76] = 4.48, p < 0.01 \)) as well as interactions of Electrode site, Laterality, and Direction (\( F[12, 228] = 4.37, p < 0.001 \)) and of Adaptation and Direction (\( F[4, 76] = 5.75, p < 0.001 \)). T-tests revealed that test stimuli with direct gaze evoked significantly less negative amplitudes when presented following direct gaze adaptation (\( M = -1.90 \mu V \)) than when presented following right gaze adaptation (\( M = -2.22 \mu V; t[19] = 2.48, p < 0.05 \), see Figure 3). Similarly, test stimuli gazing to the left evoked numerically less negative amplitudes following direct gaze adaptation (\( M = -2.32 \mu V; t[19] = 1.49, p < 0.15 \)) than following right gaze adaptation (\( M = -2.44 \mu V; t[19] = 1.48, p < 0.15 \)). In turn, test stimuli with right gaze evoked numerically less negative amplitudes following right gaze adaptation (\( M = -2.09 \mu V; t[19] = 3.10, p < 0.05 \), and an analogous trend was seen for the 5° stimuli (\( t[19] = 2.00, p = 0.06 \), uncorrected, see Figure 4).

Late positive component (P3)

In analogy to the analyses conducted in the other time windows, ERPs in the time window of 400–600 ms (see Figure 5) were analyzed in an ANOVA with the factors Site (frontal, central, parietal), Laterality (left, midline,
right), Adaptation (direct, right), and Direction of gaze in test faces (L10, L05, S00, R05, and R10).

This analysis revealed significant main effects of Site ($F[2, 38] = 68.24, p < 0.001$), Laterality ($F[2, 38] = 7.99, p < 0.01$), and Direction ($F[4, 76] = 7.77, p < 0.01$). Further, there were two-way interactions between Site and Direction ($F[8, 152] = 6.91, p < 0.001$) and Laterality and Direction ($F[8, 152] = 2.66, p < 0.05$), which were further qualified by a three-way interaction of Site, Laterality, and Direction ($F[16, 304] = 3.67, p < 0.001$).

Finally, the only significant effect of adaptation was revealed by an interaction of Adaptation and Direction ($F[4, 76] = 5.29, p < 0.01$) reflecting more positive amplitudes evoked by direct gaze test stimuli when these were presented following right as compared to direct gaze adaptation ($t[19] = 3.55, p < 0.01$). In addition, post-hoc comparisons for this interaction revealed that the relative pattern of responses evoked by the different gaze directions differed for the two different conditions of adaptation. In the baseline condition, i.e., after direct gaze adaptation, test stimuli with direct gaze evoked smallest (i.e., least positive) amplitudes, followed by stimuli gazing $5^\circ$ to the left or right, which did not differ significantly from direct gaze stimuli ($t[19] = 1.56$ and $0.98$ for $5^\circ$ left and $5^\circ$ right stimuli, respectively, both $p > 0.10$) or from each other ($t[19] = 0.91, p > 0.30$). The most positive amplitudes in the direct gaze adaptation condition were evoked by the stimuli with the largest gaze deviations, $10^\circ$ left and $10^\circ$ right, both differing significantly from the amplitudes evoked by test stimuli with direct gaze ($t[19] = 5.93$ and $4.37$ for $10^\circ$ left and $10^\circ$ right stimuli, respectively, both $p < 0.001$) and with $5^\circ$ gaze deviations ($t[19] = 4.32$ and $4.87$, both $p < 0.05$, for $10^\circ$ left vs. $5^\circ$ left and $5^\circ$ right, respectively and $t[19] = 2.82$ and $4.94$, both $p < 0.05$ for $10^\circ$ right vs. $5^\circ$ left and $5^\circ$ right, respectively).

Importantly, this pattern of larger amplitudes for test stimuli with larger gaze deviations was systematically changed after adaptation to right gaze direction. Here, stimuli gazing $5^\circ$ to the right, i.e., the adapted, direction evoked significantly smaller amplitudes than any of the other stimulus classes ($t[19] = -4.29, -3.59, 5.90, and -3.83$, all $p < 0.05$, for comparison with direct gazing stimuli, $5^\circ$ left stimuli, $10^\circ$ left, and $10^\circ$ right stimuli, respectively). Intermediate amplitudes were evoked by stimuli with direct gaze, $5^\circ$ left gaze, and $10^\circ$ right gaze directions, each differing from amplitudes evoked by test stimuli with $10^\circ$ left gaze. However, this difference failed to reach significance after correction for stimuli with direct gaze ($t[19] = -2.51, p = 0.021$, uncorrected) and $10^\circ$ right gaze ($t[19] = 2.45, p = 0.024$, uncorrected) whereas amplitudes evoked by test stimuli with $5^\circ$ left gaze were significantly different from those evoked by stimuli with $10^\circ$ left gaze following correction for multiple comparisons ($t[19] = -2.89, p < 0.05$).

**Discussion**

The current study investigated the effects of adaptation to relatively small lateral gaze deviation ($10^\circ$ right) on the perception of test stimuli showing similar deviations from direct gaze ($10^\circ$ left, $5^\circ$ left, direct, $5^\circ$ right, and $10^\circ$ right). In the present design, we ensured an equal number and timing of face presentations before each test stimulus, in order to avoid a confound between categorical face adaptation and direction-specific gaze adaptation effects on ERP responses. Thus, we chose a control condition analogously to the right adaptation condition, but consisting of “adaptation stimuli” and “top-up” stimuli with horizontally neutral (i.e., direct) gaze. Importantly, the analysis of the behavioral data revealed no differences between the response patterns obtained in a conventional pre-adaptation condition (cf. Jenkins et al., 2006; Schweinberger et al., 2007) and this new control condition, at least in the present experimental conditions (see Calder et al., 2008, for different results). This implies that, in the present study, direct gaze represents a neutral point in the representation of gaze direction and does not produce adaptation effects in itself. When seen in isolation, the present finding would be consistent with the idea that horizontal gaze direction is coded by a two-channel system, with one channel selectively coding left gaze direction and another one selectively coding right gaze direction, and with direct gaze being coded by an equilibrium of activity in the two channels. However, it needs to be noted that the present effects of adaptation to direct gaze are at variance with recent findings in a
substantial series of experiments that explicitly investigated the question of two- vs. multichannel coding of horizontal gaze direction (Calder et al., 2008). Those experiments provided consistent evidence in favor of a multichannel coding model, in which more than two separate channels (with one specific to direct gaze) code different gaze directions (Calder et al., 2008; see also Lawson, Clifford, & Calder, 2009, for similar results with...
respect to coding of body orientation). Further research may reveal whether the above discrepancies between the present study and Calder et al. (2008) could be related to small differences in experimental procedure, including factors such as the number of adaptor faces, exposure durations, or adaptor–test time intervals. While the present findings may not be easily reconciled with the idea of multichannel coding, we believe that they should not be taken to make strong theoretical claims with respect to this controversy. In particular, it needs to be kept in mind that the present study was not designed to investigate the issue of two- vs. multichannel coding of horizontal gaze direction.

The analysis of the behavioral data in the main experiment revealed clear and significant effects of adaptation to right gaze. Following adaptation, test stimuli gazing both 5° and 10° in the adapted direction were more often perceived as gazing directly at the observer than in the control condition. Further, adaptation to right gaze direction led to a decrease of incorrect “right” classifications and to an increase of incorrect “left” classifications of direct gazing test stimuli—underlining participants’ reduced sensitivity to “rightness” in gaze. Although the magnitude of these gaze adaptation effects appeared somewhat smaller as compared to those obtained with adaptation stimuli with larger gaze deviations (Jenkins et al., 2006; Schweinberger et al., 2007), our findings confirm that aftereffects of adaptation to eye gaze can be elicited by adaptors with relatively small gaze deviations equivalent to those also used at test (see also Calder et al., 2008). Based on earlier findings, we consider that such aftereffects of adaptation to eye gaze are unlikely to reflect a general bias in spatial processing, but rather are specifically related to the social directional information contained in eye gaze (Jenkins et al., 2006; Seyama & Nagayama, 2006). At the same time, it should be noted that the perception of gaze direction has been considered as a crucial component in models of social attention, which regard gaze direction as one important directional cue, together with other cues such as head or body direction. On the one hand, based on monkey single-cell recordings, a hierarchical model has been proposed in which gaze direction can “override” other directional cues from the head where these are incongruent with gaze direction and in which head cues in turn can override directional cues from body posture (Perrett, Hietanen, Oram, & Benson, 1992). On the other hand, human experimental data are more in line with the conclusion that directional head and gaze cues are mutually influencing the analysis of social attention direction (Langton, 2000). Of particular interest, adaptation-induced aftereffects similar to those seen for gaze perception were also recently reported for the perception of body (Lawson et al., 2009) and head direction (Fang, Ijichi, et al., 2007). Considering models of social attention (Nummenmaa & Calder, 2009; Perrett et al., 1992), it will be interesting for future research to determine whether such adaptation-induced directional aftereffects can transfer between different kinds of social directional stimuli (body postures, head direction, gaze direction).

The most important aim of the present study was to determine ERP correlates of direction-specific gaze adaptation. First, in line with our predictions, the present analyses provide no evidence that the N170 is sensitive to direction-specific gaze adaptation. If anything, visual inspection suggests that N170 amplitudes were slightly larger following adaptation to right as compared to direct gaze. However, any such effects were extremely small (<0.5 μV) and non-significant, and this is in strong contrast with prominent effects we found in our earlier study (3.0 μV) when comparing a classical pre-adaptation condition to both left and right gaze adaptation (Schweinberger et al., 2007). Those findings support the idea that the N170 is mainly sensitive to categorical face adaptation (Maurer et al., 2008; see also Kloth et al., 2010) and is largely unaffected by gaze direction of prior face adaptors.

In contrast, ERPs in the time range of ~250–350 ms exhibited a degree of direction-specific adaptation. In short, in the control condition (i.e., direct adaptation), occipitotemporal negativity in this time interval was smallest for test faces with direct gaze and appeared to increase approximately symmetrically with increasing horizontal deviance from direct gaze. In the right adaptation condition, however, occipitotemporal negativity was smallest for test faces with gaze in the adapted direction (cf. Figure 4). Although the latency of this effect suggests that it likely reflects a neural mechanism to tell direct from averted gaze: ERP negativity was reduced whenever eye gaze was likely to be subjectively perceived as direct. In the control condition, this was the case for direct test stimuli only, whereas following right adaptation this tended to be the case for right gazing test stimuli.

A prominent finding of the present study is that ERP correlates of directional gaze adaptation were also present in the late positive component (400–600 ms) over frontal, central, and parietal electrodes F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4. LPC amplitudes evoked by test stimuli gazing in the adapted direction were significantly less positive than those evoked by test stimuli with eye gaze directed in unadapted directions. The latency and centrotoprolateral topography of this effect suggests that it likely reflects a P3 effect, which is typically characterized by larger amplitudes in response to deviating as compared to standard stimuli (Sutton, Braren, Zubin, & John, 1965; for a recent review, see Polich, 2007). A possible account to explain the P3 effect is context-updating theory (Donchin, 1981; Donchin & Coles, 1988). This framework proposes that
the effect reflects a comparison process between the representation of a previous event in working memory and the current event. If the comparison does not result in the detection of an attribute change between stimuli, the current mental model of a stimulus is believed to be maintained. However, in the case of an attribute change, attentional processes are proposed to update the stimulus presentation, a mechanism that is reflected in a larger P3 component toward deviating stimuli.

Considering the context-updating theory of the P3, it seems plausible to assume that the current late effect might at least in part reflect easier processing of a stimulus that resembles the perceptual context provided by the adaptor stimuli (see also Kloth et al., 2010, for a similar P3 effect in a gender adaptation paradigm). The observed findings in this late time window therefore closely parallel one of the behavioral consequences of adaptation to specific stimulus attributes, which has been described as “novelty detection.” The relatively easier processing of stimuli fitting into a current perceptual context might leave more resources for the processing of deviating stimuli. Importantly, novelty may be related to adaptation via a mechanism by which adaptation improves discriminability of novel stimuli. More specifically, by attenuating responses to frequent stimuli, deviant stimuli become more salient (Kohn, 2007), an effect that may be reflected in the P3. It is worth mentioning, however, that our prediction of adaptor–test dissimilarity as the critical factor for LPC amplitude was not fully supported by the data. Crucially, following adaptation to 10° right gaze, LPC amplitude was smaller for 5° right gaze test faces, even when compared to 10° right gaze test faces. Overall, LPC amplitudes displayed a systematic pattern across conditions, with smallest amplitudes in those adaptor–test combinations that elicited high proportions of “direct” responses and largest amplitudes in those adaptor–test combinations in which gaze direction in the test face was least likely perceived as direct (cf. Figure 5).

**Conclusion**

The present study investigated neural correlates of eye gaze adaptation using ERPs. Our results show that, when categorical face adaptation is excluded as a potential confound, the N170 is insensitive to direction-specific gaze adaptation. By contrast, occipitotemporal negativity in the time interval of 250–350 ms consistently revealed direction-specific effects of gaze adaptation, suggesting the relevance of this time window for the perception of gaze direction and for the distinction between subjectively direct and averted gaze in particular. Finally, a centroparietal late positive component (400–600 ms) was also sensitive to direction-specific gaze adaptation, and LPC amplitude effects appeared to mirror increasing subjective deviance from direct gaze.

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Corresponding author: Nadine Kloth.

Email: Nadine.Kloth@uni-jena.de.

Address: Department of Psychology, Friedrich Schiller University of Jena, Am Steiger 3/Haus1, 07743 Jena, Germany.

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