

Are you looking at me? Neural correlates of gaze adaptation

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Eye gaze is an important social signal, and humans can accurately determine gaze direction in others. Recently, dramatic adaptation effects on gaze perception were shown, in which the perception of small gaze deviations to the adapted direction is diminished. We compared participants' perceptions of gaze direction before and after adaptation to the left or right gaze, and examined event-related potential correlates of this gaze adaptation. We found a striking impairment in perceiving gaze to the adapted side.

Keywords: adaptation, event-related brain potentials, eye gaze, face, N170

Event-related potentials revealed no direction-specific gaze adaptation effects on N170, although small adaptation effects were seen later, ~250–350 ms. This suggests that, rather than modulating the gaze processing ~170 ms in posterior occipitotemporal areas, adaptation modulates subsequent processes that are possibly mediated by more anterior right-temporal areas. *NeuroReport* 18:693–696 © 2007 Lippincott Williams & Wilkins.

Introduction

Efficient perception of other people's gaze direction is important for social interactions. Eye gaze is not only a key signal for exercising social control, but is also used to establish the focus of spatial attention in others. Moreover, observing the direction of gaze in others has been shown to trigger fast 'reflexive' attentional shifts in observers [1,2]. Neurophysiological research has provided evidence that gaze signals may be processed by a specific neuronal circuitry involving areas in the superior temporal sulcus. For example, cells selectively responding to different directions of gaze have been identified in macaque superior temporal sulcus [3]. Moreover, functional imaging studies suggest that regions within the superior temporal sulcus are involved in gaze perception in humans [4], and that a posterior region within the human superior temporal sulcus might be sensitive to observing eye movements in others [5].

Adaptation is a mechanism by which specific neural responses decrease after prolonged stimulation. Traditionally, adaptation effects and their neural correlates have been investigated for low-level stimulus properties, such as luminance, contrast [6], colour, or motion [7]. For instance, prolonged viewing of a downward-moving stimulus creates a powerful aftereffect, in which a static stimulus is perceived to move upward (first described by Aristotle, *Parva Naturalia*). By contrast, adaptation for complex visual stimuli has been reported only in the past decade: adaptation to a face with 'expanded' features can cause a subsequently viewed average face to be perceived as 'compressed' [8], and adaptation to an 'antiface' can even create illusory facial identity in average faces [9].

Researchers have also begun to study neural mechanisms of adaptation using functional magnetic resonance imaging [10–12] and event-related potentials (ERPs) [13]. Very recently, a powerful adaptation effect was demonstrated for the perception of eye gaze: adaptation to lateral gaze virtually eliminated the observers' perception of smaller gaze deviations in the adapted direction; gaze to that side was seen as pointing straight ahead [14,15].

In this study, we extended these novel gaze-adaptation effects by introducing a short time interval between the adaptation and the test stimuli, and investigated the neural correlates of adaptation using ERPs. We focussed primarily on the face-elicited N170, as this ERP is strongly driven by the eye region [16,17] and is thought to be at least partially generated by the posterior superior temporal sulcus region, in tasks that involve the perception of eye movements in others [18].

Methods

Participants

Ten observers (aged 19–26 years, seven women) contributed to the data. All reported normal or corrected-to-normal vision.

Stimuli

Test faces were colour photographs of 12 young adults used in an earlier study [14]. Each model posed at three gaze angles: 5° left (L05), straight (S00), and 5° right (R05) (Fig. 1). Photographs of the same 12 models gazing 25° to the left or the right were used as adaptation stimuli. Test faces

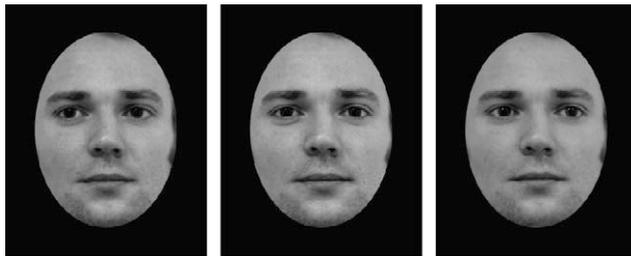
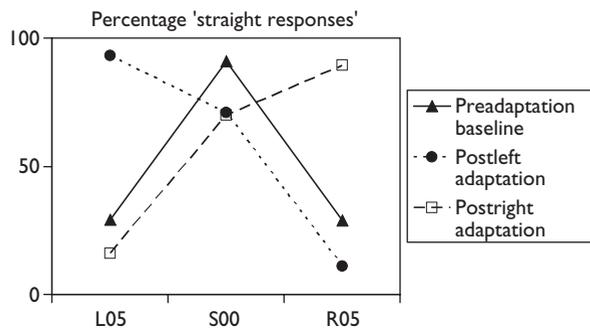


Fig 1 Percentage of 'straight' responses (mean across 10 observers) for the three different gaze angles of test faces. Examples for L05, S00, and R05 stimuli are given at the bottom of the figure, in that order, from left to right. Responses are displayed, depending on whether these faces were shown before adaptation (baseline) or after adaptation to either left or right eye gaze. See text for further details. L05, 5° left angle; R05, 5° right angle; S00, straight.

(10.3 × 17.5 cm) were presented at a viewing distance of ~87 cm, which was kept constant by using a chin rest.

Procedure

The experiment began with a 'preadaptation test' to determine the baseline ability to identify gaze direction. Using the right index, the middle, and the ring fingers on three response keys, participants indicated if a test face showed left, right, or straight gaze direction. All 36 test faces (12 identities × three gaze directions) were repeated three times in random order. For each trial, a question mark was first presented (800 ms), which was then replaced by the test face (400 ms), and followed by a blank screen for 2250 ms, during which the participants responded.

Two 'adaptation blocks' (left or right adaptation, block order counterbalanced across participants) followed the preadaptation test. In each block, 12 adaptation stimuli, with gaze averted 25° in one constant direction, were presented twice in a randomized order. The exposure duration was 3500 ms each with an interstimulus interval of 200 ms. Adaptation stimuli were presented at 90% of the size of the other stimuli so that the eye regions in the adaptation and test stimuli were nonoverlapping. This adaptation sequence was immediately followed by a 'postadaptation test'. This was the same as the preadaptation test, except that each test stimulus was preceded by two consecutive top-up adaptation displays (3500 ms each). Neither of the two top-up adaptation stimuli carried the same identity as the subsequent test face [19]. To address the issue of whether adaptation would survive for a short time interval, and to ensure a clean ERP baseline interval, a 1000-ms interval

separated the offset of the second top-up adaptation display and the onset of the test display.

Apparatus

The electroencephalogram was recorded from 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. (EasyCap, Herrsching-Breitbrunn, Germany) Electrode impedances were kept below 10 kΩ. The horizontal electrooculogram was recorded from the outer canthi of both eyes, and the vertical electrooculogram was monitored bipolarly from above and below the right eye. ERPs were recorded for 2200 ms (200 ms prestimulus baseline) and sampled at 250 Hz. Offline, trials were visually inspected for ocular (e.g. blinks, saccades) and nonocular artifacts. Trials with nonocular artifacts and saccades were discarded. For all other trials, ocular-blink contributions to the EEG were corrected using a regression method [20]. ERPs were digitally low-pass filtered at 10 Hz (zero-phase shift, 12 dB/oct), and recalculated to average reference.

Results

In the preadaptation test, participants were highly accurate at discerning direct gaze ($M=90.8 \pm 8.6\%$), and fairly accurately classified left ($M=70.3 \pm 15.6\%$) and right gaze ($M=71.0 \pm 19.2\%$). After adapting to gaze averted 25° in one direction, however, perception of gaze directed to that side was nearly eliminated ($M=3.4$ and 8.1% for left and right gaze, respectively), and gaze in the adapted direction was perceived as looking straight ahead in ~90% of trials (Fig. 1). An analysis of variance on percentages of 'straight' responses, with the factors 'adaptation' (left, right, preadapt) and 'test stimulus' (left, right, straight) revealed an interaction of adaptation and test stimulus [$F(4,36)=151.5$; $P<0.001$]. This was due to a strong increase of 'straight' responses to left-gaze test faces after left adaptation, compared with the preadaptation test [$t(9)=10.3$; $P<0.001$], and a strong increase of 'straight' responses to right-gaze test faces after right adaptation [$t(9)=8.5$; $P<0.001$].

For ERPs to test faces, we took mean amplitudes in the time segment 90–130 ms (P100) at eight occipitotemporal electrodes (O1, O2, TP9, TP10, P9, P10, PO9, PO10). Mean amplitudes for time segments 150–200 ms (N170) and 250–350 ms were taken at eight posterior electrodes (P7, P8, TP9, TP10, P9, P10, PO9, PO10).

Analogous analyses of variance as for behavioural data were run, with additional factors for electrode site and hemisphere. We observed a significant effect of adaptation on the P100 [$F(2,18)=6.7$, $P<0.01$]. Although P100 amplitude was significantly more positive after both left-adaptation and right-adaptation relative to the preadaptation test ($P<0.01$), P100 amplitude was equivalent after left-adaptation and right-adaptation blocks ($P>0.20$). Similarly, although there was an effect of adaptation on the N170 amplitude, both as a main effect [$F(2,18)=4.5$; $P<0.05$] and as an interaction with site [$F(6,54)=15.5$; $P<0.001$], this was entirely due to the fact that the N170 amplitude was significantly smaller following both the left-adaptation and right-adaptation relative to the preadaptation test (Fig. 2). N170 was equivalent for left-adaptation and right-adaptation blocks ($P>0.20$).

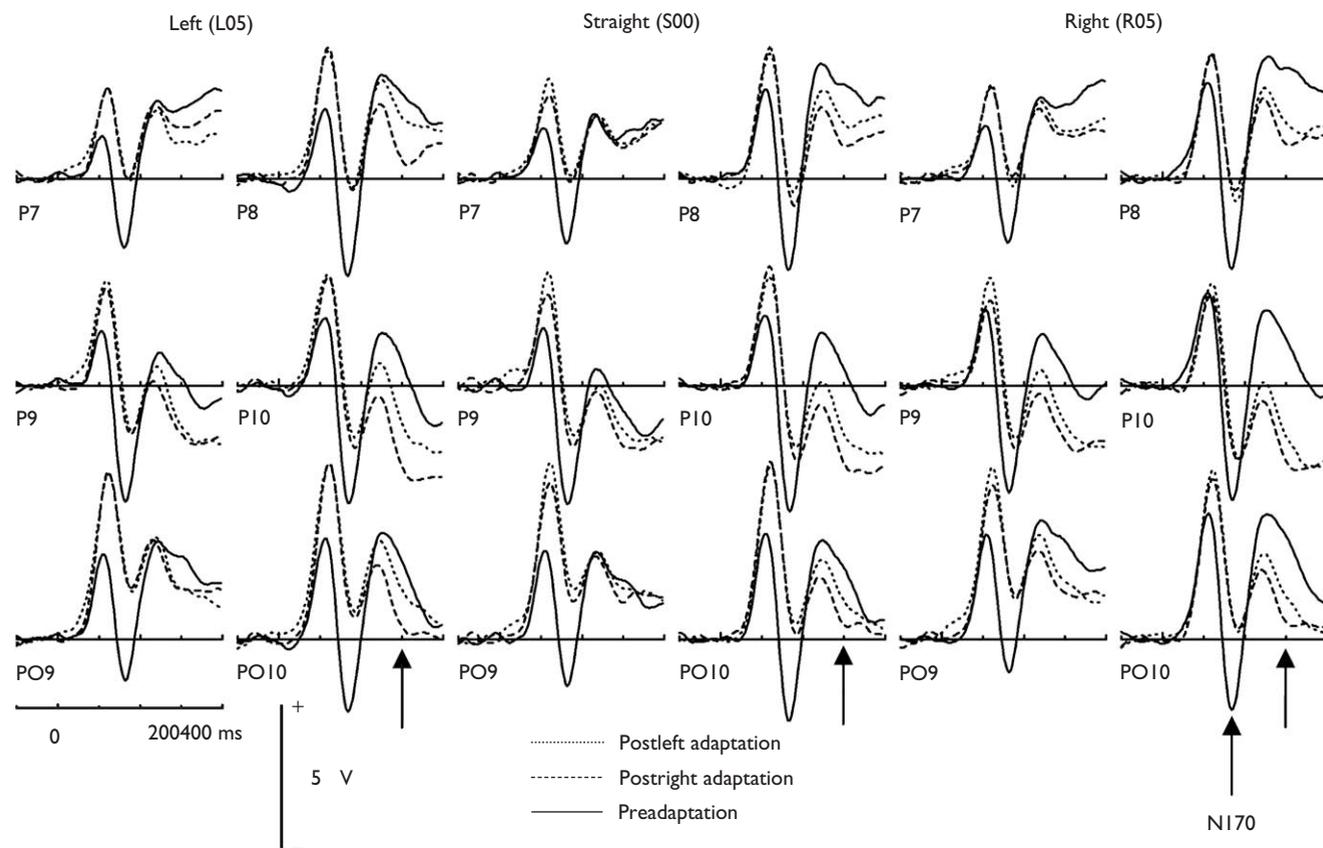


Fig 2 Grand average event-related potentials (ERPs) across 10 observers, for the three different gaze angles of test faces, depending on whether these faces were shown before adaptation (preadaptation baseline) or after adaptation to either left or right eye gaze. Recordings are shown for a selected set of posterior electrodes. Arrows indicate the N170 and the larger right positivity ~250–350 ms after adaptation to left vs. right eye gaze. See text for further details.

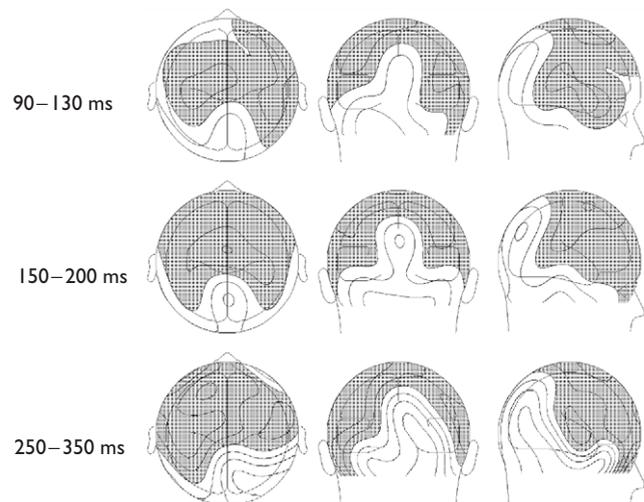


Fig 3 Voltage maps (spherical spline interpolation, 110° equidistant projection) for the ERP differences (left-adaptation minus right-adaptation) averaged across test stimuli. Positivity is white, negativity is shaded. Isocontour lines are separated by 0.25 V. Note the right posterior positivity ~250–350 ms and the absence of direction-specific adaptation effects in the preceding time segments.

Peak latencies of P100 and N170 were determined at PO10 (80–150 ms and 130–220 ms windows). Effects of adaptation on P100 latency [$F(2,18)=51.3, P<0.001$] reflected shorter

latencies for preadaptation blocks ($M=122.4\pm 6.8, 123.7\pm 8.5,$ and 111.3 ± 7.3 ms for left-adaptation, right-adaptation, and preadaptation, respectively). No further effects or interactions were found ($P>0.20$), and there were no differences between left-adaptation and right-adaptation blocks ($P>0.20$). Effects of adaptation on N170 latency were also significant [$F(2,18)=17.3; P<0.001$], again with shorter latencies for preadaptation blocks ($M=186.9\pm 17.3, 189.3\pm 19.1,$ and 170.4 ± 13.5 ms for left-adaptation, right-adaptation, and preadaptation blocks, respectively). No further effects or interactions were found ($P>0.20$), and there were no latency differences between left-adaptation and right-adaptation blocks ($P>0.20$).

The 250–350 ms segment was the only time segment that revealed ERP differences between left-adaptation and right-adaptation blocks [$F(3,27)=3.5; P<0.05$] for the interaction adaptation by site, owing to a right posterior positivity following left-adaptation vs. right-adaptation (Figs 2 and 3). Note that this effect was similar across the test stimuli, and there was no interaction involving test stimulus ($P>0.20$).

Discussion

We demonstrated a striking adaptation effect to lateral eye gaze. The ability to perceive small gaze deviations was virtually eliminated after adaptation to gaze strongly diverted into the same direction. Intriguingly, the present

adaptation effect was of similar size to the effect by Jenkins *et al.* [14], despite the fact that we introduced a 1 s interval between the adaptation and the test stimulus, indicating that gaze adaptation effects persist for a short time interval. The precise time course of gaze adaptation, however, is unclear as yet, and researchers have only now begun to study the time course of adaptation for other facial aspects [21].

Despite the striking effects of gaze adaptation on the perception of test stimuli, and although the N170 has been linked to the perception of eyes [16,17], N170 was completely unaffected by the direction of the earlier gaze adaptation. Assuming that the current N170 in gaze perception is generated by the posterior superior temporal sulcus regions [18]; this suggests that gaze adaptation does not modify processing ~170 ms in those regions. Note that despite the prominent role of the eye region for the N170, the sensitivity of N170 for gaze direction is also controversial; effects of gaze direction (straight vs. left) on N170 amplitude were seen in some studies, but not in others [22–24].

Although we observed no direction-specific effects of gaze adaptation on N170, we could elicit smaller and more delayed N170 responses to the same test faces during the postadaptation blocks than during the preadaptation block. This unexpected finding may be tentatively ascribed to the fact that test faces were shown >3000 ms after an earlier test face in the preadaptation block, but only 1000 ms after an earlier top-up adaptor face in postadaptation blocks. The reduced and delayed N170 in postadaptation blocks might thus reflect the adaptation of a mechanism that is sensitive to the detection of facelike stimuli (irrespective of specific information such as gaze, sex, or identity), and which is reflected in N170 [19]. This interpretation can be reconciled with earlier results on adaptation for other types of facial information [13]; nevertheless, this issue deserves further investigation. An implication for studies using ERPs (N170) to investigate facial adaptation, however, is that these should use adaptation conditions that differ with respect to the relevant information only (e.g. for gaze adaptation, left vs. direct vs. right gaze adaptors; for sex adaptation, male vs. androgynous vs. female adaptors), whereas faces are used as adaptors throughout.

Despite the absence of direction-specific gaze adaptation on N170, there was a later adaptation effect ~250–350 ms over the right posterior regions. This may be an interesting parallel to a very recent functional magnetic resonance imaging study of gaze adaptation, which also reported no adaptation effects on the posterior superior temporal sulcus regions, whereas adaptation effects were found in more anterior superior temporal sulcus regions, and in the inferior parietal cortex [25]. Overall, the current findings suggest that adaptation does not modify gaze processing ~170 ms in posterior superior temporal sulcus regions, but alters subsequent processes that may be mediated by more anterior temporal areas of the right hemisphere.

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