Adaptation to vergent and averted eye gaze

Ben Stiel

School of Psychology & Australian Centre of Excellence in Vision Science, The University of Sydney, Sydney, Australia

Colin W. G. Clifford

School of Psychology & Australian Centre of Excellence in Vision Science, The University of Sydney, Sydney, Australia

School of Psychology, The University of New South Wales, Sydney, Australia

Isabelle Mareschal

School of Psychology & Australian Centre of Excellence in Vision Science, The University of Sydney, Sydney, Australia

School of Biological and Chemical Sciences, Psychology, Queen Mary University of London, London, UK

Previous adaptation studies have revealed the tuning properties of mechanisms coding left-right averted gaze. Here, Experiment 1 used an adaptation procedure to investigate the mechanisms that encode vergent eye gaze. Following prolonged exposure to convergent or divergent gaze, observers were more likely to categorize smaller gaze deviations in the adapted direction as parallel (i.e., nonvergent). We then examined whether adaptation was occurring to the eyes independently (monocular gaze direction) as opposed to the two eyes as a unitary stimulus (binocular gaze direction). In Experiment 2, we interleaved presentations of convergent and divergent adaptors and tested with either congruent (vergent) or incongruent (left-right) stimuli. Similarly, we interleaved presentations of leftward- and rightward-averted adaptors and tested with congruent (left-right) and incongruent (vergent) stimuli. If adaptation were driven solely by monocular gaze direction, congruent and incongruent adaptation would be similar because, at the level of an individual eye, the stimuli are identical. We find considerable adaptation in the incongruent conditions, consistent with adaptation to individual eye directions. However, we also find greater adaptation in congruent conditions, implicating the involvement of mechanisms that encode binocular gaze direction.

Introduction

The ability to interpret the direction of a person's eye gaze is an important skill in social interaction (Friesen & Kingstone, 1998) as it communicates a wealth of information about a person's focus and mental state (Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & Walker, 1995). It is important to establishing joint attention (Moore & Dunham, 1995), and it can function to assert social dominance (Kleinke, 1986). Eye gaze even has the capacity to "hijack" an observer's attention by reflexively reorienting it in the direction of the initiator's gaze (Friesen & Kingstone, 1998). Identifying the functional mechanisms that contribute to the interpretation of gaze is important to understanding the role it plays in communication in healthy people and developing strategies to assist people with impaired gaze processing (Leekam, Baron-Cohen, Perrett, Milders, & Brown, 1997).

How do we estimate the direction of a person's gaze? Anstis, Mayhew, and Morley (1969) proposed that judgments of direction of gaze are determined principally by the position of the pupil in the visible part of the eye. However, psychophysical investigations have shown that head orientation can influence the perceived direction of gaze (Anstis et al., 1969; Cline, 1967; Gibson & Pick, 1963). Anstis et al. noted that turning the head with gaze fixed on a given point

(e.g., directly ahead) changes the visible part of the eye. The account of Anstis et al. suggests that gaze should consistently be perceived in the direction opposite to the head turn as found by Gibson and Pick (1963). However, it has also been reported that "head-position and eye-position interact to produce a perceived direction which falls between these two positions" (Cline, 1967, p. 50; Langton, Honeyman, & Tessler, 2004; Wollaston, 1824), demonstrating that head orientation has a direct influence on perceived direction of gaze over and above its influence on the visible part of the eye (Langton et al., 2004; Todorovic, 2006). More recently, effects beyond eye direction and head orientation have been shown to influence gaze perception. For example, it has been shown that we have certain assumptions (a priori) about another person's direction of gaze that bias our perception of a slightly averted gaze as being directed toward us (Mareschal, Calder, & Clifford, 2013). Here, we use stimuli with a fixed (direct) head orientation and vary the horizontal position of each eye to control the direction and vergence of gaze.

The physiological examination of gaze has demonstrated that separate populations of neurons in the superior temporal sulcus (STS) of macaque monkeys respond differentially to direct and averted gaze, indicating that direct and nondirect gaze are processed through distinct neural channels (Perrett et al., 1985). Lesioning the STS in monkeys results in significant gaze-processing deficits, including reduced ability to discern gaze direction (Campbell, Heywood, Cowey, Regard, & Landis, 1990; Eacott, Heywood, Gross, & Cowey, 1993). A patient presenting with focal damage to the superior temporal gyrus exhibited a tendency to perceive gaze to the right of the actual line of sight as well as impaired attention to gaze (Akiyama et al., 2006). Imaging studies report an association between the posterior STS and processes involved in discerning intentionality from a person's gaze direction (Friesen & Kingstone, 1998; Pelphrey, Viola, & McCarthy, 2004). More recently, Calder et al. (2007) combined imaging and adaptation and found that separate neural channels in the STS encode leftward- and rightward-averted gaze.

Psychophysical adaptation studies provide important insight into the functional mechanisms underpinning gaze perception. Adaptation refers to a process whereby prolonged exposure to a stimulus affects the subsequent perception of similar stimuli (Clifford & Rhodes, 2005). In general, this manifests as reduced sensitivity to the adapted stimulus or a perceptual bias (Webster & MacLeod, 2011). This effect is thought to reflect a change in the activation of neurons in the visual cortex that selectively respond to the adapting stimulus (Kohn, 2007). Psychophysics has made extensive use of this

phenomenon to study the way the visual system codes features, such as color (Bartleson, 1978), orientation (Gibson & Radner, 1937), and motion (Levinson & Sekuler, 1976).

Recent studies demonstrate that adaptation is also evident in response to more complex stimuli, such as body position (Lawson, Clifford, & Calder, 2009), facial emotions (Hsu & Young, 2004), distortion of facial features (Webster & MacLin, 1999), and gender (Barrett & O'Toole, 2009; Webster, Kaping, Mizokami, & Duhamel, 2004). Recently, adaptation has also been applied to gaze perception, revealing that repeated exposure to gaze in a specific direction affects the subsequent ability to identify gaze in that direction (Calder et al., 2007; Cheleski, Mareschal, Calder, & Clifford, 2013; Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006). In these studies, following prolonged exposure to images of faces with eyes averted to the right or left, participants demonstrated an increased tendency to judge gaze that is averted in the direction of adaptation as being direct. Perception of gaze deviations in the nonadapted direction remained largely unaffected. These effects persisted over variations in head size and head orientation between adaptation and test phases, indicating that they are not the result of retinal or early cortical habituation. Rather, they support a model of higher-level visual processes that respond specifically to a representation of gaze direction (Jenkins et al., 2006).

Experiment 1 aimed to investigate whether observers adapt to vergent gaze, following the procedure of Jenkins et al. (2006). Figure 1a illustrates how adaptation to vergent gaze is hypothesized to affect observers' perception of gaze. The solid purple line represents the cone of parallel vergence, the range of eye-gaze vergences that observers judge as being parallel (and forward facing). This terminology is akin to the cone of direct gaze (Gamer & Hecht, 2007) that corresponds to the range of gaze deviations that observers judge as being direct. Following adaptation to convergent (dashed blue) or divergent (dashed red) gaze separately, it is hypothesized that observers' cones of parallel vergence will be shifted in the direction of the adaptor because, using gaze direction instead of vergence, it has been found that adaptation makes slight deviations in the adapted direction appear direct (e.g., Calder, Jenkins, Cassel & Clifford, 2008).

Although adaptation studies have provided important insights into the neural mechanisms underlying perception of gaze direction, the precise nature of the stimulus attributes that are being encoded remains unclear; specifically, at the perceptual level, what constitutes "gaze"? To date, studies investigating gaze adaptation have done so only as a binocular gaze direction. An underlying assumption is that the
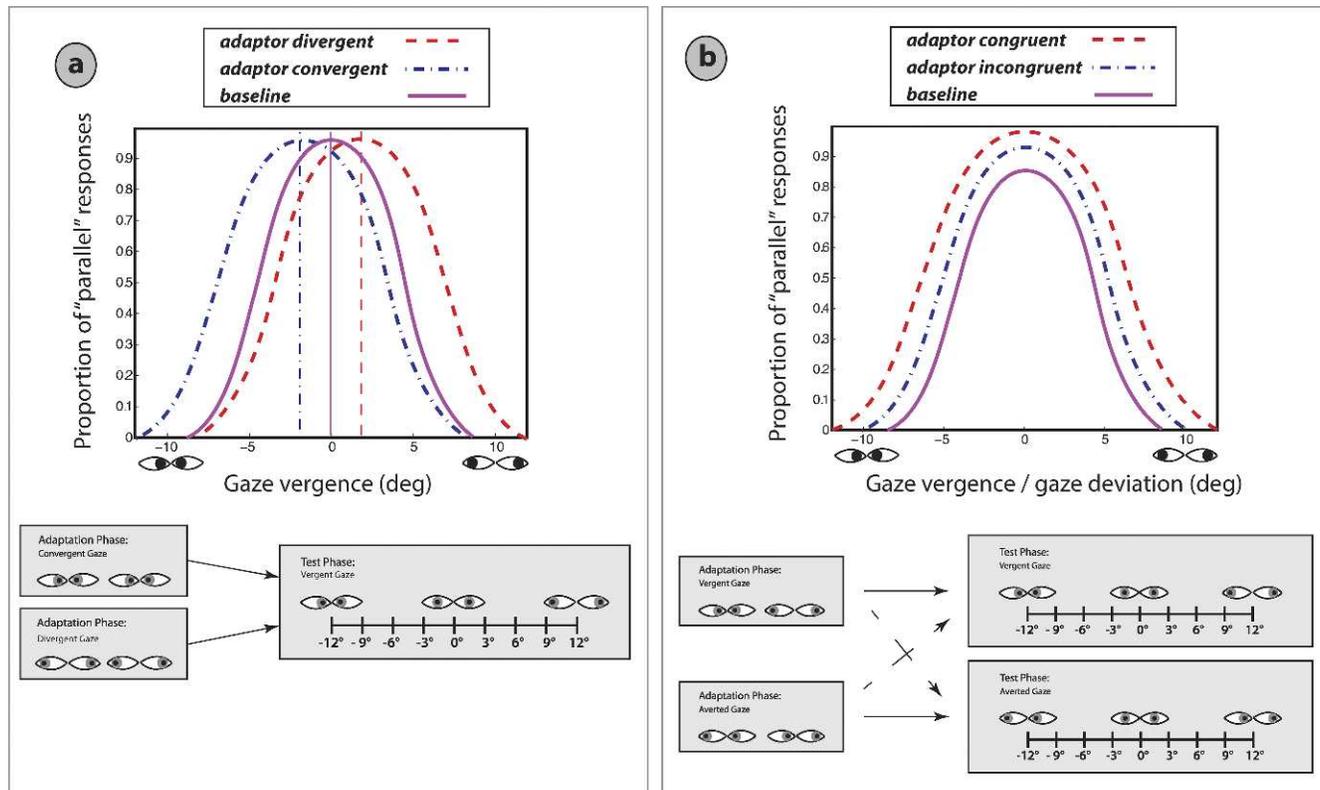
Figure 1. Anticipated change in the cones of parallel vergence following adaptation. (a) In Experiment 1, adaptation to convergent gaze of 20° is predicted to cause a slightly convergent gaze to appear more parallel (dashed blue curve) whereas adaptation to divergent gaze of 20° (dashed red curve) is predicted to cause slightly divergent gaze to appear more parallel. (b) In Experiment 2, the cone of parallel vergence (for vergent test stimuli) is predicted to increase if the observer is adapted to incongruent stimuli (left-right averted, blue curve) but to increase more if the observer is adapted to congruent stimuli (vergent, red curve).

adaptive stimulus consists of the two eyes processed together as a unitary stimulus as has been claimed for gaze-cuing effects (Hietanen & Yrttimaa, 2005). Another possibility, however, is that individual eyes are registered as monocular gaze stimuli, and adaptation reflects the sum of adaptation to each eye individually. To test whether adaptation occurs to binocular gaze direction, we examined whether interleaved adaptation using congruent stimuli (adaptor and test are both vergent or averted) was greater than adaptation using incongruent stimuli (adaptor and test are vergent and averted, respectively, or vice versa, e.g., Figure 1b). It has been shown (using left-right averted stimuli) that adaptation to the interleaved presentation of leftward and rightward gaze directions leads to an increase in the cone width, such that slight leftward and rightward deviations are more frequently classified as direct (Calder et al., 2008). If an observer is only adapting to monocular gaze direction, congruent and incongruent stimuli should result in an equal amount of adaptation because, at the level of an individual eye, vergent and averted stimuli are identical. If, however, there were also adaptation occurring at a level at which binocular

gaze direction is encoded, this would produce greater adaptation effects in congruent than incongruent conditions.

Methods

Apparatus and stimuli

A Dell XPS computer running MATLAB™ (Math-Works, Ltd.) was used for stimulus generation, experiment control, and recording subjects' responses. The programs controlling the experiment incorporated elements of the PsychToolbox (Brainard, 1997). Stimuli were displayed on a Sony Trinitron 20SE monitor (1024 × 768 pixels, refresh rate: 75 Hz) driven by the computer's built-in NVIDIA GeForce GTS 240 graphics card. The display was calibrated using a photometer and linearized using look-up tables in software. At the viewing distance of 57 cm, 1 pixel subtended 2.2 arcmin. Two authors and six naïve volunteer subjects participated in the study. One naïve observer's data were discarded because he failed to

Adaptation Block
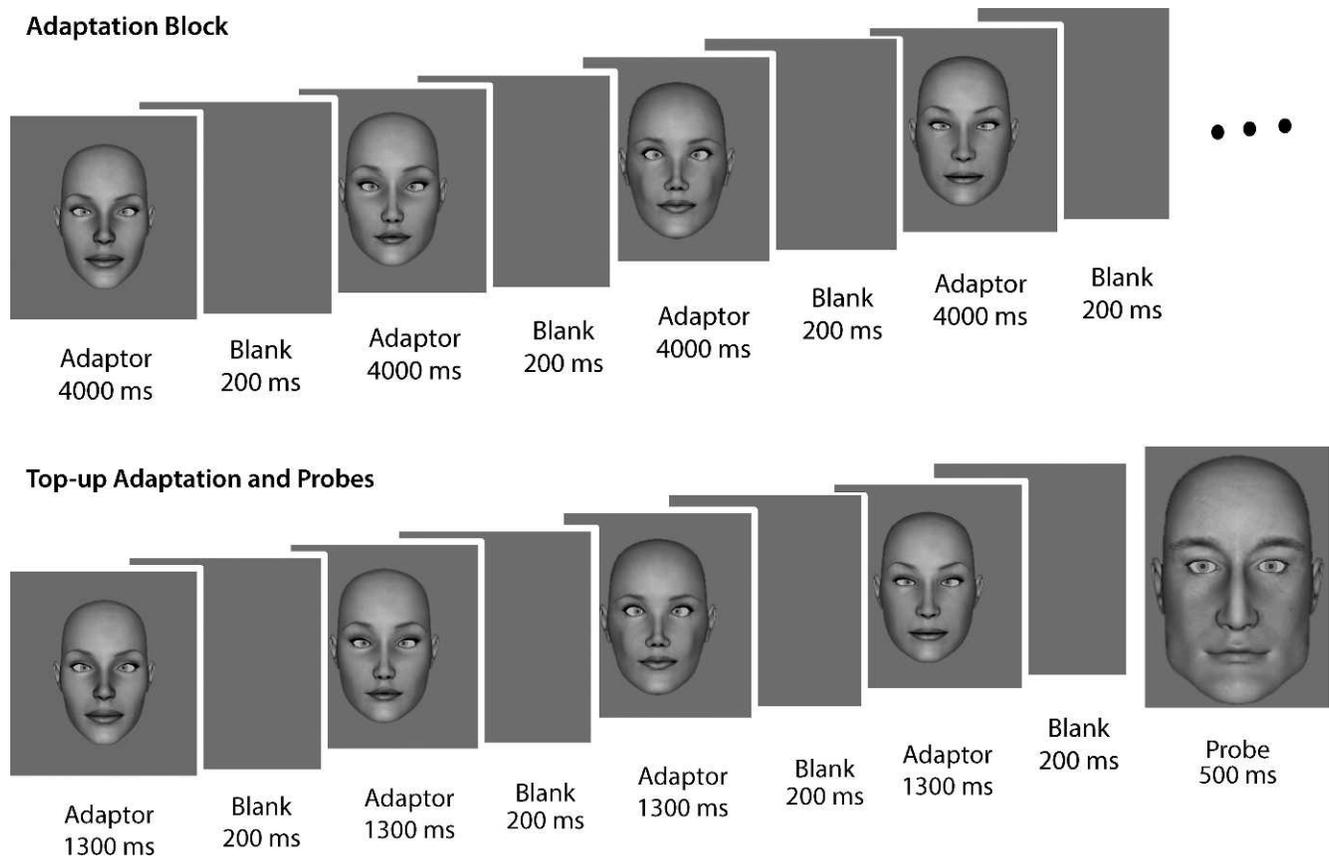

Top-up Adaptation and Probes

Figure 2. Adaptation procedure used in Experiments 1 and 2. The observer adapted to repeated presentations of a gaze stimulus (shown here is noninterleaved 20° convergent for Experiment 1) for 1 min, followed by a top-up phase that lasted 6000 ms, and was then tested with a probe face of opposite gender. Following this first trial, only the top-up and test sequence lasting 6000 ms were shown for the remaining trials in the run.

perform the task as instructed by only attending one eye in the face. Inspection of his data revealed no clear evidence of adaptation in the standard interleaved (left/right averted) task. All experiments adhered to the declaration of Helsinki guidelines.

Grey scale images of eight synthetic faces created using Daz software (http://www.daz3d.com/) (four male, four female) were presented (sample face shown in Figure 2). The eyes were deviated equally in opposite directions for the vergent stimuli, from convergent to divergent, or in the same direction for averted stimuli from leftward to rightward. The size of the faces in visual angles subtended was 15° × 11° on average. The deviations of the eyes were controlled in Matlab, and participants reported the gaze deviation of the faces using the "4," "5," and "6" keys. For trials measuring judgment of left/right averted gaze, these keys indicated left, direct, and right gaze, respectively. For trials testing judgment of vergent gaze, these keys corresponded to convergent, direct, and divergent gaze, respectively. In order to avoid confusion between conditions, in the following (text and figures) we refer

to the "direct" condition when testing vergence as "parallel."

Procedure

Experiment 1 measured the amount of adaptation to noninterleaved vergent stimuli. Experiment 2 measured whether adaptation to congruent stimuli was greater than adaptation to incongruent stimuli following interleaved adaptation. Baseline measurements (preadaptation and postadaptation) were obtained before all experiments commenced and at the very end of Experiment 2. In the averted condition, the prebaseline and postbaseline measures were compiled to determine the average range of gaze deviations that each observer judged as being direct (termed the cone of direct gaze). In the vergence condition, prebaselines and postbaselines were measured to determine the average range of gaze vergences that each observer judged as being parallel (e.g., no vergence, termed the cone of parallel vergence). Adaptation was expected to change the cone of

parallel vergence, shifting its peak (Experiment 1) or increasing its width (Experiment 2).

Measuring baselines

Baselines were measured for each observer in two blocks of trials (using male and female faces, separately). Observers judged the direction of vergence (convergent/divergent) or gaze (left/right). Subjects could make one of three responses: "convergent," "divergent," or "parallel" (for vergence stimuli) and "left," "right," or "direct" for averted stimuli using key presses. Gaze deviations/vergences were presented using a method of constant stimuli selected from the following range ($-12°$, $-6°$, $-3°$, $-1°$, $0°$, $1°$, $3°$, $6°$, $12°$) in which negative values correspond to leftward or convergent gaze and positive values are rightward and divergent. Each gaze deviation/vergence was sampled 12 times in a run (four faces × three repeats). During each trial, faces were presented for 500 ms followed by a 600-ms blank screen presentation after which participants could indicate their judgment of gaze direction/vergence. The order of testing averted and vergent gaze, as well as the gender, was counterbalanced across participants.

Participants' responses were compiled across runs and logistic functions were fitted to the proportion of "left" and "right" responses (for the averted stimuli) or "convergent" and "divergent" (for the vergent stimuli). A function for "direct" (or "parallel") responses was calculated by subtracting the summed proportions of the "left" and "right" ("convergent" and "divergent") responses from one (see Mareschal, Calder, Dadds, & Clifford, 2013 for the first description of this method). These three functions were fitted as an ensemble using the Nelder-Mead simplex method (Nelder & Mead, 1965) implemented via Matlab's fminsearch function to minimize residual variance. The separation between the crossover points of the "direct" and the "left" (or "parallel" and "convergent"), and "direct" and "right" (or "parallel" and "divergent") responses, respectively, is taken as the cone of direct (or parallel) gaze.

Measuring adaptation

Experiment 1: Adaptation to noninterleaved vergent gaze stimuli: Experiment 1 consisted of two sections: one in which participants adapted to convergent gaze angled at $-20°$ and another in which they adapted to divergent gaze angled at $+20°$. Two runs were collected for each section, one using female faces as adaptors and male faces as tests and the other using males faces as adaptors and female faces as tests.

A run began with an adaptation phase in which a series of four virtual faces, all with convergent or all with divergent gaze deviations, were shown four times

each for 4000 ms with a 200-ms grey screen between presentations. This was followed immediately by a "top-up" adaptation that lasted 6000 ms with each adaptor face shown for 1300 ms separated by a 200-ms grey screen interval. The test face was of opposite gender and 33% larger to reduce low-level adaptation (e.g., Calder et al., 2008; Jenkins et al., 2006; Seyama & Nagayama, 2006) and was presented for 500 ms, followed by a grey screen until the observer's response. After the first trial (adaptation followed by top up), all following trials only consisted of the top-up phase followed by the test. This is illustrated schematically in Figure 2.

Test gaze stimuli (directions or vergences) were presented using a method of constant stimuli from the same range as for the baselines ($-12°$, $-6°$, $-3°$, $-1°$, $0°$, $1°$, $3°$, $6°$, $12°$). One run consisted of a total of 108 trials (four test faces × nine gaze stimuli × three repeats) with equal presentations of each gaze stimulus and each face identity. The order in which participants completed convergent and divergent adaptation conditions and the assignment of the gender of the stimuli to adaptation and test conditions were counterbalanced across participants.

Experiment 2: Adaptation to interleaved vergent or averted gaze stimuli: This experiment employed a technique similar to that developed by Calder et al. (2007), who showed that adapting to interleaved presentations of leftward and rightward gaze deviations resulted in a greater range of gaze deviations being judged as direct (i.e., a broader cone of direct gaze). This experiment had two types of adaptation: incongruent adaptation and congruent adaptation. For incongruent adaptation, the observer adapted to interleaved presentations of convergent and divergent gaze and was tested with averted gaze (and vice versa, adapted to interleaved presentations of leftward- and rightward-averted gaze and was tested with vergent gaze). For congruent adaptation, the observer adapted to interleaved convergent and divergent gaze vergences and was tested with vergent gaze (and, similarly, he or she adapted to interleaved leftward- and rightward-averted stimuli and was tested with averted gaze). The presentation of the adapting and test stimuli was similar to Experiment 1 and consisted of an adaptation phase lasting 1 min, followed by top-up adaptation and then the test (see Figure 2). In the top-up phase, four faces were presented for 1300 ms each, followed by a blank screen for 200 ms and then the probe stimulus for 500 ms. Participants performed two runs per condition, and the order of presentation of conditions was counterbalanced across participants. Observers could perform adaptation to congruent or incongruent stimuli within the same day of testing, but a break of at least 2 hr was imposed before testing with a different

	Convergent crossover		Midpoint		Divergent crossover	
	Mean	SE	Mean	SE	Mean	SE
Baseline	−5.29	0.43	−0.50	0.29	+4.27	0.65
Adaptation to convergent gaze	−9.91	0.92	−3.31	0.69	+3.29	0.98
Adaptation to divergent gaze	−5.19	0.86	+1.92	0.40	+9.03	0.77

Table 1. Category axes and midpoints. *Notes*: Values are in degrees.

adaptor to avoid transfer of effects between the two conditions.

Results

Experiment 1

The cone of parallel vergence was measured following convergent and divergent adaptation: Widths and midpoints are reported in Table 1. After convergent adaptation, there is a clear shift in the crossover points between convergent and parallel as well as a shift in the midpoint. Following adaptation to divergent gaze, there is also a shift in the midpoints and divergent crossover. This is clearly visible in Figure 3, which plots the average adaptation and baseline (compiled preadaptation and postadaptation) data across all observers. Note that adaptation to convergent stimuli (blue curve and triangles) or divergent stimuli (red curve and circles) shifts the cone in the direction of the adaptor.

Paired samples one-tailed t tests were performed to investigate differences in mean cone midpoints between convergent and divergent adapted cones. The results indicated a significant difference between the cone
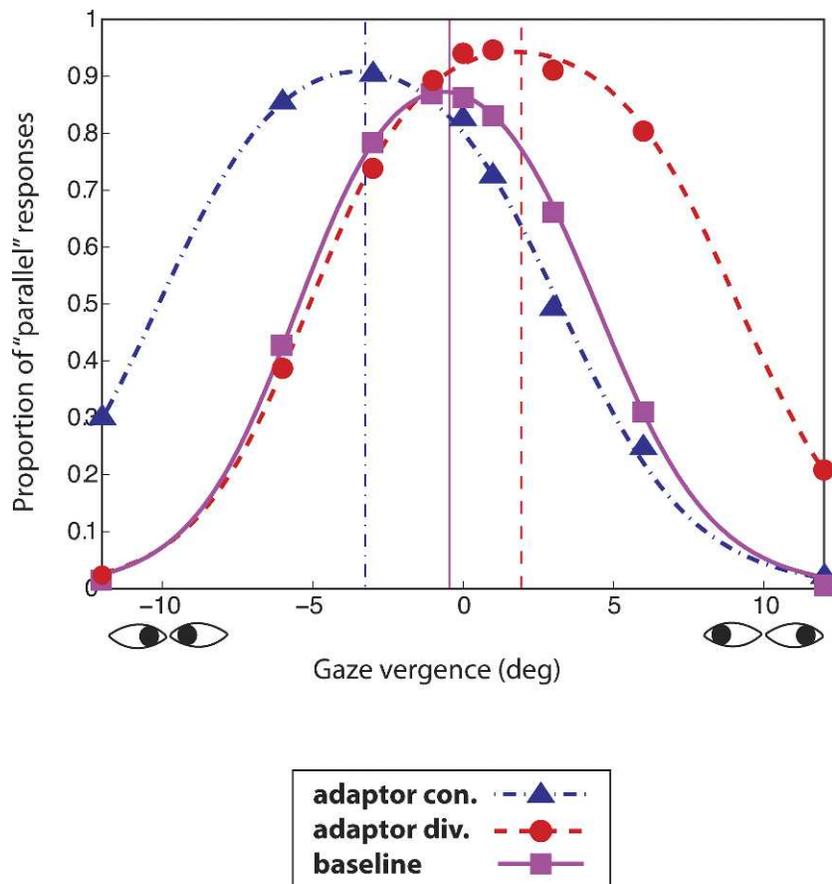

Figure 3. Cones of parallel vergence fitted to the compiled data. Solid purple curve is the unadapted baseline, circles and dashed red curve are the cone following divergent adaptation, and triangles and dashed blue are the cone following convergent adaptation. In both cases, the midpoints of the cones after adaptation (dotted vertical blue and red curves) are shifted away from the unadapted midpoint (solid purple) toward the adaptor.
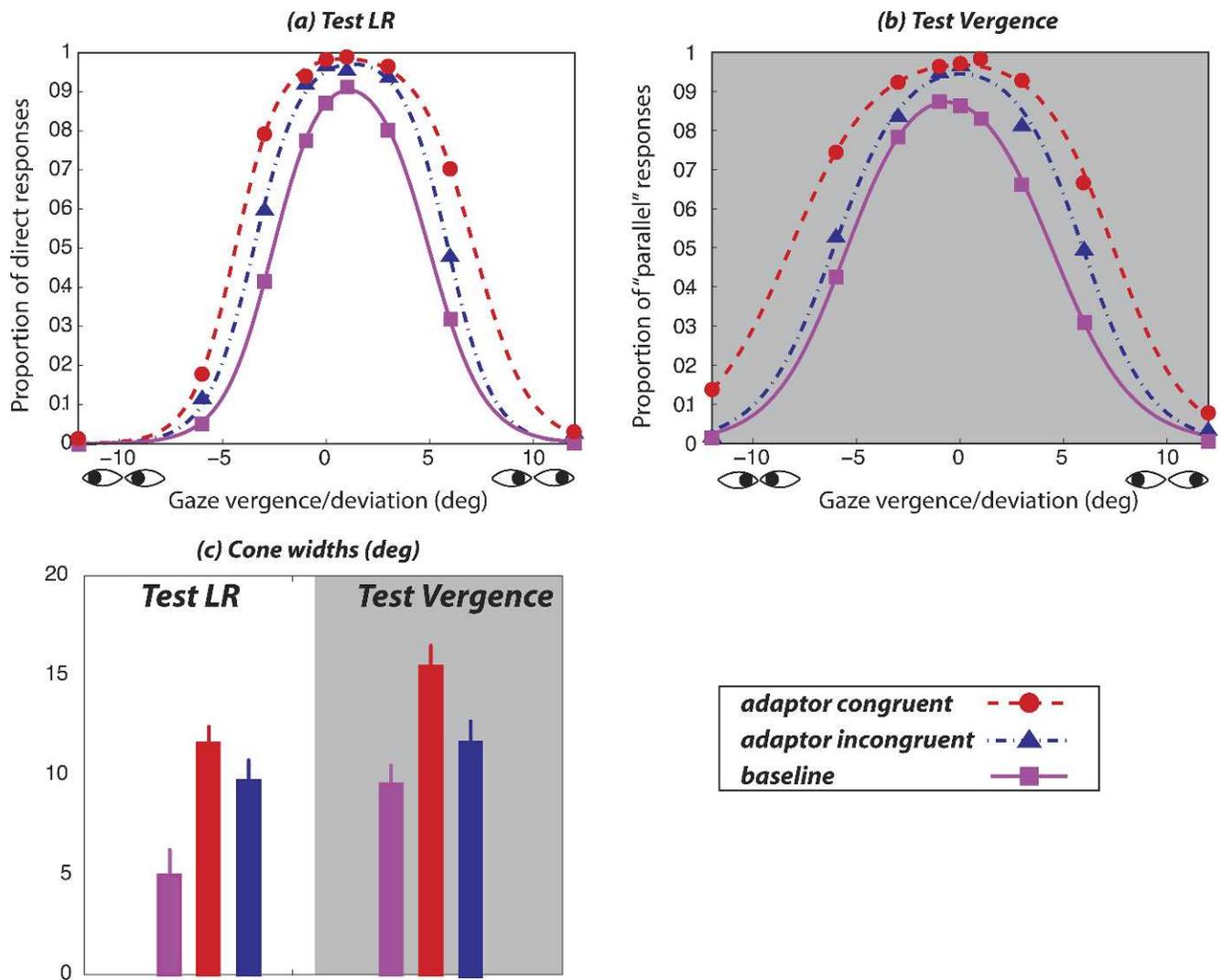
Figure 4. (a) Cone of direct gaze fitted to the compiled data when the test was left-right averted. (b) Cone of parallel vergence when the test was convergent-divergent. Solid purple curves are the unadapted baselines, dashed blue (triangles) is the cone following incongruent adaptation, and dashed red (circles) is the cone following congruent adaptation. In both cases, the cones are wider following congruent adaptation compared to incongruent adaptation. (c) Average cone widths across observers with one standard error.

midpoints after adaptation to convergent gaze compared to divergent gaze of 5.24°, $t(6) = 5.23$, $p < 0.001$, $d = 3.53$.

Relative to baseline, there was a shift in the cone midpoint toward the adapted direction of 2.81° after adaptation to convergent gaze, $t(6) = 5.92$, $p < 0.001$, $d = 2.73$, and a shift of 2.43° after adaptation to divergent gaze, $t(6) = -3.59$, $p < 0.001$, $d = 2.64$.

Experiment 2

The cone of direct/parallel gaze was measured for averted and vergent gaze in both congruent and incongruent adaptation conditions. In both cases, the width of the cones increased (more so when the test was

vergent) in the congruent conditions. This can be seen in Figure 4, which plots the average data when the test was (a) left-right averted gaze and when the test was (b) vergent gaze. Cone widths for the different conditions are presented as a bar graph in Figure 4c. Solid lines (square symbols) are average baselines, dashed blue lines (triangles) are when the adaptor was congruent, and dashed red lines (circles) are when the adaptor was incongruent.

A 2×2 ANOVA was conducted on the data from the four adapted conditions. Mean cone width for tests of vergent gaze was 2.86° greater than that for averted gaze, averaged across adaptation to vergent and averted gaze, $F(1, 6) = 15.46$, $p = 0.008$, $\eta_p^2 = 0.72$. This can be easily visualized by comparing panels (a) and (b) in Figure 4. Of particular importance, the main effect

for adaptation condition was significant, such that mean cone widths were 2.88° greater when adaptor and test presentations were congruent than when they were incongruent, averaged across tests of vergent and averted gaze, $F(1, 6) = 25.00$, $p = 0.002$, $\eta_{p}^2 = 0.81$. The interaction term was not significant, indicating that the increase in cone width did not differ markedly between vergent and averted adaptors averaged across tests, $F(1, 6) = 1.39$, $p = 0.284$, $\eta_{p}^2 = 0.19$.

One-tailed t tests were conducted to investigate simple effects, indicating an effect for tests of averted gaze, such that when testing averted gaze, the width of the direct gaze cone was 1.94° greater following adaptation to averted gaze relative to vergent gaze, $t(6) = -3.03$, $p = 0.012$, $d = 0.77$. The simple effect for tests of vergent gaze was also significant, indicating that when testing vergent gaze, the width of the parallel vergence cone was 3.81° greater following adaptation to vergent gaze as compared to averted gaze, $t(6) = 3.10$, $p = 0.011$, $d = 1.40$.

A one-tailed paired samples t test compared baseline cone widths, indicating that cones of parallel vergence were significantly wider than cones of direct gaze by an average of 4.6° prior to adaptation, $t(6) = 2.83$, $p = 0.015$, $d = 1.56$. Baseline cone widths were also compared with incongruent adapted conditions using one-tailed t tests. Cone widths for tests of vergent gaze after adaptation to left-/right-averted gaze were, on average, 2.10° wider than the baseline cones, $t(6) = 2.70$, $p = 0.018$, $d = 3.65$. Cone widths for tests of left-/right-averted gaze after adaptation to vergent gaze were an average of 4.76° wider than baseline cones, $t(6) = 3.65$, $p = 0.005$, $d = 1.55$, suggesting that incongruent adaptation did cause an increase in cone widths.

Discussion

Experiment 1 investigated whether observers can adapt to gaze vergence. We find that, following repeated exposure to either convergent or divergent gaze at 20°, observers were more likely to perceive vergence in the adapted direction as being parallel (i.e., nonvergent). This provides evidence that convergent and divergent gaze can be differentially adapted, indicating that these gaze configurations are processed by separable neural channels.

Experiment 2 examined the independent contribution of each eye to adaptation (monocular gaze direction) compared to the impact of the two eyes together as a unitary stimulus (binocular gaze direction). We found that the width of the cone of direct/parallel gaze was greater for congruent than incongruent adaptation conditions, demonstrating that the adaptive influence of the eyes individually was markedly less than that of both eyes together. The influence of monocular gaze adaptation is not null, however, as incongruent adaptation led to a cone of direct gaze significantly broader than baseline. It is worth noting that, when adapting to left-right averted gaze, the vergence is always parallel whereas, when adapting to vergent gaze (in the convergent condition only), the gaze is perceived as forward (or direct). This raises the possibility that there is some adaptation of a parallel vergence channel in the left-right adaptation condition and, conversely, some adaptation of a direct gaze channel in the vergent adaptation condition. Any such effects would be expected to reduce the proportion of direct or parallel responding in the incongruent conditions relative to the congruent, perhaps contributing to the significance of the differences that we observe. However, the effects of adapting a direct channel have been found to be quite small (Calder et al., 2008), suggesting that any effects that may arise would be fairly minimal. Furthermore, any such effects would necessarily be occurring at the level of binocular gaze representation and thus do not challenge our fundamental conclusion that a significant component of adaptation must be occurring at the binocular level.

Interestingly, the effect of the congruence of adaptation is not homogenous in the two test conditions. We find greater differential effects of congruent versus incongruent adaptation for judgments of vergent gaze compared to left-right averted gaze. This may reflect a difference in the nature of vergent and averted gaze stimuli. For example, the perception of vergent gaze can only be obtained by looking at both eyes together. Although viewing only one eye may create an impression of vergent gaze if the observer has an expectation that the other eye is pointing in the opposite direction, this impression must be derived rather than explicitly perceived. In contrast, given the frequency of left-right averted gaze, it is likely that a leftward or rightward gaze direction may be signaled by only one eye. To our knowledge, how observers judge gaze direction when only one eye is viewed remains unexplored. It may well be that the default response to a single eye stimulus would be to interpret the gaze as averted in the direction of the eye, particularly for large deviations (see Figure 5). If so, the binocular gaze stimulus would be less important to the perception of averted gaze compared to vergent gaze. The smaller effect of congruency when testing judgments of left-right averted gaze may therefore reflect participants' reduced reliance on the binocular gaze stimulus in this condition relative to tests of vergent gaze.

Although the angle of convergence shown in the adaptation stimuli may represent an extreme alignment, it nevertheless remains a possible configuration for people with normal binocular vision. On the other hand, divergent gaze is not compatible with binocular

Figure 5. Examples of faces presenting only one eye. The image on the left could be interpreted as either a left-right averted gaze deviated leftward or a convergent gaze or some combination of averted and convergent gaze. The image on the right could be interpreted as a left-right averted gaze deviated leftward or (less likely) as a divergent gaze or a combination of averted and convergent gaze.

vision as it prohibits integration of stereoscopic information from the two eyes. Indeed, divergent gaze stimuli appear unnatural and may be ambiguous in their signaling of gaze direction. Interestingly, in the present study, we find no evidence for a difference between divergent and convergent adaptation (Experiment 1). This result appears at odds with a study by Robbins, McKone, and Edwards (2007), who found that unnatural manipulations of eye configuration generated less adaptation than more naturalistic distortions.

This study used a behavioral paradigm to investigate the determinants of adaptation in human eye gaze. For the first time, judgments of convergent and divergent gaze were shown to be selectively susceptible to adaptation after exposure to eye stimuli in these configurations. Of particular importance, we found evidence of adaptation to the two eyes as a unitary stimulus beyond the effect of adaptation to each eye independently. This may reflect neural plasticity at a stage of processing that encodes the mental representation of gaze. Overall, these findings indicate that the separate components of gaze stimuli that contribute to adaptation are synergistic, rather than merely additive. In other words, gaze is greater than the sum of its parts.

Keywords: gaze, adaptation, vergence

Acknowledgments

Corresponding author: Isabelle Mareschal.
Email: i.mareschal@qmul.ac.uk.
Address: School of Biological and Chemical Sciences, Psychology, Queen Mary University of London, London, UK.

References

Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Nakachi, R., & Kashima, H. (2006). A deficit in discriminating gaze direction in a case with right superior temporal gyrus lesion. *Neuropsychologia*, *44*(2), 161–170.

Anstis, S. M., Mayhew, J. H., & Morley, T. (1969). The perception of where a face or television 'portrait' is looking. *American Journal of Psychology, 82,* 474–489.

Baron-Cohen, S., Campbell, R., Karmiloff-Smith, A., Grant, J., & Walker, J. (1995). Are children with autism blind to the mentalistic significance of the eyes? *British Journal of Developmental Psychology*, *13*(4), 379–398.

Barrett, S. E., & O'Toole, A. J. (2009). Face adaptation to gender: Does adaptation transfer across age categories? *Visual Cognition*, *17*(5), 700–715.

Bartleson, C. J. (1978). A review of chromatic adaptation. In F. W. Billmeyer, Jr., & G. Wyszecki, Eds., *AIC Proceedings, Color 77,* Troy, NY (pp. 63–96). Bristol, UK: Adam Hilger.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*(4), 433–436.

Calder, A. J., Beaver, J. D., Winston, J. S., Dolan, R. J., Jenkins, R., & Eger, E. (2007). Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Current Biology, 17*(1), 20–25.

Calder, A. J., Jenkins, R., Cassel, A., & Clifford, C. W. G. (2008). Visual representation of eye gaze is coded by a nonopponent multichannel system. *Journal of Experimental Psychology: General, 137*(2), 244.

Campbell, R., Heywood, C., Cowey, A., Regard, M., & Landis, T. (1990). Sensitivity to eye gaze in prosopagnosic patients and monkeys with superior temporal sulcus ablation. *Neuropsychologia*, *28*(11), 1123–1142.

Cheleski, D. J., Mareschal, I., Calder, A. J., & Clifford, C. W. G. (2013). Eye gaze is not coded by cardinal mechanisms alone. *Proceedings of the Royal Society, B, 280,* 1–7.

Clifford, C. W., & Rhodes, G. (2005). *Fitting the mind*

to the world: Adaptation and after-effects in high-level vision (Vol. 2). Oxford, UK: Oxford University Press.

Cline, M. G. (1967). The perception of where a person is looking. *American Journal of Psychology, 80,* 41–50.

Eacott, M., Heywood, C., Gross, C., & Cowey, A. (1993). Visual discrimination impairments following lesions of the superior temporal sulcus are not specific for facial stimuli. *Neuropsychologia, 31*(6), 609–619.

Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review, 5*(3), 490–495.

Gamer, M., & Hecht, H. (2007). Are you looking at me? Measuring the cone of gaze. *Journal of Experimental Psychology: Human Perception and Performance, 33,* 705–715.

Gibson, J. J., & Pick, A. D. (1963). Perception of another person's looking behaviour. *American Journal of Psychology, 76,* 386–394.

Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology, 20*(5), 453.

Hietanen, J., & Yrttimaa, K. (2005). Where a person with a squint is actually looking: Gaze-cued orienting in crossed eyes. *Visual Cognition, 12*(1), 117–126.

Hsu, S. M., & Young, A. W. (2004). Adaptation effects in facial expression recognition. *Visual Cognition, 11*(7), 871–889.

Jenkins, R., Beaver, J. D., & Calder, A. J. (2006). I thought you were looking at me: Direction-specific aftereffects in gaze perception. *Psychological Science, 17*(6), 506–513.

Kleinke, C. L. (1986). Gaze and eye contact: A research review. *Psychological Bulletin, 100*(1), 78.

Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *Journal of Neurophysiology, 97*(5), 3155–3164.

Langton, S. R. H., Honeyman, H., & Tessler, E. (2004). The influence of head contour and nose angle on the perception of eye gaze direction. *Perception & Psychophyiscs, 66,* 752–771.

Lawson, R. P., Clifford, C. W. G., & Calder, A. J. (2009). About turn: The visual representation of human body orientation revealed by adaptation. *Psychological Science, 20*(3), 363–371.

Leekam, S., Baron-Cohen, S., Perrett, D., Milders, M., & Brown, S. (1997). Eye-direction detection: A dissociation between geometric and joint attention skills in autism. *British Journal of Developmental Psychology, 15*(1), 77–95.

Levinson, E., & Sekuler, R. (1976). Adaptation alters perceived direction of motion. *Vision Research, 16*(7), 779–781.

Mareschal, I., Calder, A. J., & Clifford, C. W. G. (2013). Humans have an expectation that gaze is directed toward them. *Current Biology, 23,* 1–5.

Mareschal, I., Calder, A. J., Dadds, M. R., & Clifford, C. W. (2013). Gaze categorization under uncertainty: Psychophysics and modeling. *Journal of Vision, 13*(5):18, 1–10, http://www.journalofvision.org/content/13/5/18, doi:10.1167/13.5.18. [PubMed] [Article]

Moore, C., & Dunham, P. J. (1995). Current themes in research on joint attention. *Joint attention: Its origins and role in development* (pp. 15–28). Hillsdale, NJ: Lawrence Erlbaum & Associates.

Nelder, J. A., & Mead, R. (1965). A simplex method for function minimization. *The Computer Journal, 7*(4), 308–313.

Pelphrey, K. A., Viola, R. J., & McCarthy, G. (2004). When strangers pass: Processing of mutual and averted social gaze in the superior temporal sulcus. *Psychological Science, 15*(9), 598–603.

Perrett, D., Smith, P., Potter, D., Mistlin, A., Head, A., & Milner, A. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London. Series B. Biological Sciences, 223*(1232), 293–317.

Robbins, R., McKone, E., & Edwards, M. (2007). Aftereffects for face attributes with different natural variability: Adapter position effects and neural models. *Journal of Experimental Psychology: Human Perception and Performance, 33*(3), 570.

Seyama, J., & Nagayama, R. S. (2006). Eye direction aftereffect. *Psychological Research, 70*(1), 59–67.

Todorovic, D. (2006). Geometrical basis of perception of gaze direction. *Vision Research, 46,* 3549–3562.

Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature, 428*(6982), 557–561.

Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1571), 1702–1725.

Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review, 6*(4), 647–653.

Wollaston, W. H. (1824). On the apparent direction of eyes in a portrait. *Philosophical Transactions of the Royal Society of London, 114,* 247–256.