

A Direct Link Between Gaze Perception and Social Attention

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How information is exchanged between the cognitive mechanisms responsible for gaze perception and social attention is unclear. These systems could be independent; the “gaze cueing” effect could emerge from the activation of a general-purpose attentional mechanism that is ignorant of the social nature of the gaze cue. Alternatively, orienting to social gaze direction might be directly determined by the operation of cognitive mechanisms specifically dedicated to gaze perception. This second notion is the dominant assumption in the literature, but there is little direct support for this account. Here, we systematically manipulated observers’ perception of gaze direction by implementing a gaze adaptation paradigm. Gaze cueing was reduced only in conditions where perception of specific averted gaze stimuli was impaired (Experiment 1). Adaptation to a pointing stimulus failed to impact gaze cueing (Experiment 2). Overall, these data suggest a direct link between the specific operation of gaze perception mechanisms and the consequential orienting of attention.

Keywords: gaze perception, adaptation, social attention, gaze cueing

It is crucial that we explore our environment to ensure we select important stimuli for further processing. The cognitive system therefore has evolved highly efficient attentional mechanisms for fluent search. Moreover, humans are social beings, and as such need to select and rapidly process social information. Personally and socially relevant information of great importance—even survival value—can be gleaned from monitoring the attention systems of other people by determining their gaze direction. Following the gaze of another person and thus establishing “joint attention” could yield new information about useful objects or resources in the environment. Further, joint attention affords the generation of inferences about the mental state of the other person (Moore & Dunham, 1995). The focus of the present study is to establish whether the mechanism responsible for the conscious perception of gaze direction is directly involved in the generation of attention shifts in the direction of observed gaze.

Baron-Cohen (1995) proposed three modules underpinning a range of social perception abilities, one of which he termed the “Eye Direction Detector” which some argue is innate, given evidence that a preference for gaze stimuli is measurable just 36 hours after birth (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000). This theoretical module can operate on simple heuristics to determine the direction of another’s gaze (Langton, Watt,

& Bruce, 2000). The simplicity is possible due to the unique morphology of the human eye, with the high contrast between the iris and the sclera, and between the sclera and the eyelids (Kobayashi & Kohshima, 1997). Hence, we are able to make highly accurate gaze direction judgments (Gibson & Pick, 1963), but are greatly impaired when the gaze stimulus is presented with inverted contrast (i.e. iris and pupil are white with a black sclera) despite the preservation of geometrical properties of the stimulus (Ricciardelli, Baylis, & Driver, 2000). The neurophysiological work of Perrett and colleagues in the macaque superior temporal cortex suggests that gaze perception is achieved via the activity of populations of neurons that are specifically tuned to observed gaze direction (Perrett et al. 1992).

Gaze Perception

Recent work on gaze perception in humans has advanced our understanding of how the human cognitive system determines the direction of observed gaze. A powerful approach introduced by Jenkins, Beaver, & Calder (2006) uses an adaptation technique to explore the functional mechanisms of gaze perception. In their experiments, participants are asked to make judgments about the gaze direction of faces appearing on a computer screen. Preceding these judgment tasks, however, participants are exposed to a stream of faces consistently looking only to the right or the left. Given sufficient time, this exposure biases subsequent perception of the “test” gaze stimuli. Specifically, participants become more likely to judge a face looking 5° or 10° in the direction to which they are adapted as looking straight ahead. For example, after repeated exposure to faces looking 25° to the left, a face looking 5° or 10° in that direction now appears as if it is looking straight at you, rather than over your shoulder. This effect has been replicated numerous times (e.g. Calder, Jenkins, Cassel, & Clifford, 2008; Kloth & Schweinberger, 2008; Seyama, 2006; Seyama & Nagayama, 2006; Teufel et al. 2009).

Adaptation to gaze direction is thought to reflect the existence of at least three types of cells that code gaze direction in the human

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brain. Under this “multichannel coding” account, perception of observed gaze direction is derived from the relative activity of cells coding eyes to the left, right, and direct gaze (see Calder et al., 2008). If we see eyes looking to the right, activity of right-coding cells is high; left- and direct-coding cells, conversely, fire at a baseline level. Thus the aggregate output from the cell population leads to the perception of rightward gaze. However, after adaptation to a particular stimulus class, the firing rate of cells coding that stimulus is reduced. The net output from these cells is weaker, resulting in a signal that is harder to disambiguate from straight gaze, leading to impaired judgments. This behavioral evidence is supported by an functional magnetic resonance imaging (fMRI) experiment using similar adaptation logic to the BOLD response, which also reduces following repeated activation of a region of the brain (Calder et al., 2007). Regions in the anterior superior temporal sulcus (STS) and in the inferior parietal lobule (IPL) were identified as candidate regions for the location of the left/right/direct gaze-sensitive cells.

Gaze-Cueing of Attention

The behavioral impact of observing averted gaze on attention has similarly garnered the interest of several research groups (Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999; Langton & Bruce, 1999; see Frischn, Bayliss, & Tipper, 2007, for review). In cognitive experiments inspired by developmental studies of joint attention (e.g. Scaife & Bruner, 1975) but utilizing spatial attention paradigms (e.g. Posner, 1980), a face is presented looking either left or right. The participant is asked to respond to a target that might appear either at the looked-at (valid) or the invalid location. Quicker reaction times for validly cued targets are taken as evidence for an automatic shift of attention to the looked-at location.

One important question is whether or not gaze-triggered orienting is fundamentally unique in terms of the underlying attentional processes that give rise to gaze following behavior. Does gaze cueing of attention arise from the activation of gaze-specific networks such as those described above? Conversely, one could just as easily posit that a general orienting mechanism that is blind to fact that gaze stimuli are cues to another persons attentional state is responsible for gaze cueing effects (see Figure 1). That is, these specialized mechanisms for gaze perception may be important for

consciously determining where someone is looking, and the socio-emotional consequences of that perception (e.g. threat detection), but may not necessarily be directly providing the signals upon which attention shifts are generated.

While the first account is may be more intuitive, there is actually little direct evidence in support of this account, and little to convincingly reject the second notion. Firstly, it is notable that spatially uninformative gaze cues elicit a basic cueing effect which is behaviorally indistinguishable in terms of magnitude, temporal signature and individual differences, from shifts caused by arrow cues (e.g. Bayliss, di Pellegrino, & Tipper, 2005; Bayliss & Tipper, 2005; Downing, Dodds, & Bray, 2004; Tipples, 2002; Tipples, 2008). Similarly, gaze cues and arrow cues activate broadly overlapping brain areas (Sato, Kochiyama, Uono, & Yoshikawa, 2009; but see Hietanen, Nummenmaa, Nyman, Parkkola, & Hämäläinen, 2006). Finally, it is significant that Calder et al. (2007) identified an *anterior* portion of the STS as a patch of human cortex containing cells coding gaze direction, as to our knowledge no human neuroimaging study investigating social attention has implicated this region. Instead most studies find activity in the *posterior* section of the STS (e.g. Materna, Dicke, & Thier, 2008; see Allison, Puce, & McCarthy, 2000 and Nummenmaa & Calder, 2009, for discussion). Data from Pelphrey, Singerman, Allison, and McCarthy (2003; see also Piermo et al. 2008) suggest the pSTS region is involved in higher level aspects of social attention, such as deriving intentions from observing gaze behavior, and as such might not be responsible for the low-level analysis of gaze direction that might be sufficient to influence attention. Therefore, it is currently difficult to establish a clear picture of the mechanisms directly contributing to joint attention behaviors from current neuroimaging work.

There is some evidence for differences in top-down control of gaze and arrow cueing (Friesen, Ristic, & Kingstone, 2004; Ristic & Kingstone, 2005; but see Tipples, 2008). However, it is important to note that these data do not imply that the bottom-up representations on which the attention system acts during gaze or arrow cueing are different in any way. Gaze cueing could simply emerge through the perception of stimulus asymmetry common to many directional stimuli (see Downing, Dodds, & Bray, 2004) and executed by an attention system that is blind to the social content of the stimulus (Materna et al. 2008). Therefore, on the basis of

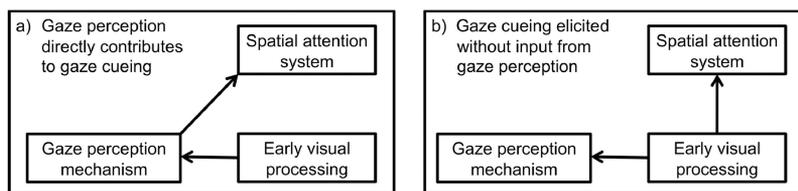


Figure 1. Schematics of two possible ways that gaze cueing could emerge. a) A dedicated gaze perception system outputs information about the direction of observed gaze to an attention orienting system, which shifts attention on the basis of these signals to the corresponding location in space. b) Gaze cueing occurs without reference to the operation of the gaze perception system; the alternative posited here (one of many) is that earlier visual analysis of the asymmetric eye stimulus that contains high-contrast boundaries is sufficient for the attention system to act on gaze stimuli as cues to attention. Clearly, intermediate processing stages could be invoked in either hypothetical system; but this report focuses only on the role (or lack thereof) of a direct link between the gaze perception and spatial orienting systems.

current data, the specialized mechanism for gaze perception that has been identified empirically (Calder et al., 2008) and included in theoretical models of social perception (Baron-Cohen, 1995) need not be implicated in a model of gaze cueing.

The Current Study

The aim of this paper is to establish convincing evidence for a direct role of gaze perception mechanisms in the generation of the gaze cueing effect. Such evidence would allow us to confidently place a specialized gaze perception mechanism at the centre of a model of the gaze cueing effect. Some previous reports have approached this question. For example, one study has shown that when gaze perception is impaired by contrast negation, overt gaze following is also disrupted (Ricciardelli, Betta, Pruner, & Turrato, 2009). However, contrast negation is a drastic manipulation of the stimulus that may disrupt fluent perception globally; when the system is confronted with such stimuli it is difficult to infer precisely how encoding is affected in a mechanistic manner. A second source of evidence again hints towards a direct role for gaze perception in gaze cueing. Kingstone and colleagues report data from callosotomy patients demonstrating that while arrow cues presented in both hemifields influenced attention in these patients, gaze cues produced significant cueing effects only when presented to the face processing-dominant hemisphere in the same patients (Kingstone, Friesen, & Gazzaniga, 2000). If we assume that gaze perception is also lateralized in the same way as face perception is, then this suggests that gaze cueing can only occur when the hemisphere that is better equipped to encode gaze direction can project to the attention system. While this is evidence against a general orienting mechanism acting on gaze cues, we need behavioral evidence from normal adults to confirm these indicative findings. More specifically, by deriving specific predictions from the detailed model of gaze perception outlined by Calder et al. (2008), we aim to demonstrate a systematic influence of the activation of a specialized gaze perception system on gaze cueing of attention.

We utilized Jenkins et al.'s (2006) gaze adaptation paradigm to manipulate observers' perception of averted gaze cues. We then examined whether this manipulation affects the magnitude of the attention shift elicited. Hence, we adapted participants to faces gazing 25° to the left or to the right, then presented them with gaze cues subtending either 17.5° or 10°. Our predictions were as follows: If the attention system does not act on signals directly derived from the activity of the gaze perception system, then adapting to gaze direction will have no impact on attention whatsoever. That is, 17.5° and 10° gaze cues will be effective cues to attention whether they are looking in the adapted direction (even though they often explicitly reported to appear to be direct gaze) or in the unadapted direction. Alternatively, if gaze cueing arises from the unmodulated aggregate output from the gaze perception system, then the gaze cueing effects will be affected in a highly predictable and specific manner. That is, weak gaze cues (i.e. 10°) in the adapted direction will propagate an ambiguous signal to the attention system, resulting in a weak cueing effect, whereas strong gaze cues in this direction (17.5°) will cue attention effectively as the signal will be less adversely affected by the adaptation procedure. Conversely, cues in the opposite direction to the adapting stimuli will elicit strong gaze cueing effects whether weak (10°) or

strong (17.5°), assuming the multi-channel account favored by Calder et al. (2008).

Using this procedure to investigate this question has a number of advantages. Firstly, we can make specific predictions about the interaction between gaze perception and attention systems. It is crucial we can do this without altering the physical cue stimulus presented to participants across conditions. Secondly, the gaze adaptation procedure has been shown previously to specifically target the gaze perception system in isolation. For example, adaptation to gaze direction is robust across changes in identity, size, head orientation in the picture and rotational planes, ruling out low level stimulus effects as the source of the aftereffect (Jenkins et al., 2006; Seyama, 2006). Critically for our present purposes, adapting to gaze does not influence spatial perception per se (Jenkins et al., 2006), and adapting to other directional stimuli does not influence gaze perception (i.e. arrows; Seyama & Nagayama, 2006). These features of the gaze adaptation paradigm make it an excellent tool for application to this problem. We can therefore use this approach to confirm that gaze cueing relies on gaze perception mechanisms rather than being derived from parallel activity at an earlier domain-general stage of visual processing.

To preempt the key findings: Experiment 1a establishes that our stimulus set produces reliable effects of gaze adaptation on perception of gaze direction, such that gaze looking 10° in the adapted direction is often perceived as direct gaze. Next, Experiment 1b demonstrates that this manipulation of perception of gaze has a commensurate effect on attention. That is, if one no longer overtly perceives a deviated gaze cue as containing directional information, the gaze cue fails to cause a shift of attention in the actual direction of gaze. Experiment 2 shows that adaptation to an equivalent social cue (a pointing gesture) does not lead to modulation of the *gaze*-cueing effect. Together, these data are strong evidence for the contribution of a direct link between the mechanisms underlying gaze perception and social attention.

Experiment 1a

The first experiment was designed to test whether our set of stimuli could elicit effects of adaptation on gaze perception, before Experiment 1b investigates the impact of adaptation on gaze cueing. Previous work has shown strong effects of adaptation on gaze directions shifted 5° from direct, with weaker yet reliable effects at 10° (e.g. Jenkins et al., 2006). However, we considered that using 5° of deviation may not be enough to trigger a shift of spatial attention, in the critical Experiment 1b. It was important therefore to establish that our stimuli elicit reliable gaze adaptation effects on the perception of 10° of deviation of gaze.

In the adaptation phase, participants were shown a series of faces looking 25° to the left or right. The participants then completed a three alternative forced choice gaze perception task (left/straight/right) on faces gazing either straight ahead (0°), 17.5° to the left or right, or 10° to the left or right. Performance on this gaze perception task before adaptation (baseline) was compared with when the adapting stimuli were left or right gazing faces. As in previous work with this paradigm, we used the proportion of "straight" responses to each stimulus type as the critical measure (e.g. Jenkins et al., 2006). Greater "straight" responses to 10° deviations of gaze are expected when the gaze is in the same direction as the preceding adapting stimuli as compared with when

the test stimulus is looking in the opposite direction to the adapting stimuli.

Method

Participants

Sixteen female undergraduates (mean age 18.9 years, $SD = 1.5$) from the School of Psychology, University of Queensland, completed the experiment in return for course credit. All were naïve as to the purpose of the study and gave informed consent.

Stimuli

Eight models (four males, four females) were photographed looking straight ahead, and 10° , 17.5° , and 25° to the left and right with their head oriented directly towards the camera (seven photos per model). Additional photos were taken with the eyes closed. The 25° photographs were cropped within an oval shape subtending 11.2 cm in height by 9.0 cm wide and displayed in grayscale on a black background. The eyes measured approximately 0.8 cm \times 2.0 cm. The eyelid regions of the ‘eyes closed’ stimuli were pasted onto each of these 25° gaze stimuli to create a further set of faces that when presented briefly would give the impression of an eyeblink. The other photographs (17.5° , 10° , and 0°) were cropped to a smaller size, 8.4 cm \times 6.6 cm, and the eyes measured approximately 0.5 cm \times 1.5 cm. Each stimulus was flipped left-right so as to produce an additional set of mirrored stimuli. A fixation cross measuring 0.5 cm \times 0.5 cm was placed on the screen at the approximate location of the bridge of the nose of the face stimuli. The word “respond,” in capitals, measuring 0.7 cm high was presented as a prompt to participants, one was 6.0 cm above and another 8.4 cm below the fixation cross. Stimulus presentation was controlled by E-Prime 1.2 software and presented on 40-cm monitors placed approximately 57 cm away from the participants.

Design

The experiment employed a within-subjects design, with two factors. “Adaptation condition” had three levels, “Unadapted baseline,” “Adapted Left,” and “Adapted Right.” The second factor was “Gaze direction” with five levels: “ 17.5° left,” “ 17.5° right,” “ 10° left,” “ 10° right,” and “ 0° direct.” The dependent measure, as in previous reports of this effect, was the proportion of “straight” responses to each gaze stimulus under the three adaptation conditions in a three alternative forced choice (left, straight, right) gaze perception task.

The eight stimulus faces were split into two groups of four (2 males, 2 females in each). For half the participants, the first group of faces served as adapting stimuli, and the second as test stimuli. This assignment was reversed for the other participants. Original or mirrored orientation of the gaze stimuli was also counterbalanced between subjects. All participants completed a block of gaze judgment trials prior to exposure to any adapting stimuli as a baseline measure of performance. Following this, participants were either adapted to the left then to the right, or in the opposite order (counterbalanced across subject). Hence there were eight experimental procedures, assigned randomly to participants. This

counterbalancing served to reduce the impact of any spurious stimulus- or order-based effects in the overall results.

Procedure

Participants were seated in a dimly lit room in groups of up to four (separated by booth dividers), and instructed to keep their eyes at the location of the fixation cross during the task. On “test” trials, participants were told that they would see faces appear in the centre of the screen and that their task was to judge quickly and accurately the direction that the eyes were looking. Responses were made with three fingers of the right hand, with the numbers 1, 2, and 3, corresponding to “left,” “straight,” and “right,” respectively, on the keypad of a keyboard. On each of these trials, a fixation cross was presented for 500 ms, followed by the probe face, accompanied by the word “respond” in two locations for 500 ms. From the onset of this stimulus, participants had 2000 ms to respond to the direction of gaze. A blank screen followed the offset of the face for 2000 ms before the next trial. The identity of the face and the direction of gaze were selected randomly on each trial. During adaptation blocks, participants were instructed to fixate as usual and respond with a tap on the spacebar should they see a face blink. The adapting block consisted of displays of randomly-selected faces looking only in one direction for 4000 ms. On 12.5% of displays, the impression of a blink was produced by presenting the eyes-closed version of the face for the middle 400 ms of the total stimulus duration. Participants had until the offset of the stimulus to respond to the blink (i.e. 1800 ms). These blinks were present to ensure participants attended to the eye region of the stimuli. Examples of stimuli and trial progressions are given in Figure 2.

F2

Experimental sessions began with a 20-trial practice gaze judgment block, followed by 120 trials assessing baseline gaze perception performance (24 trials for each of the five gaze directions). After this block, participants observed a 32-stimulus adaptation block while detecting blinks (128 seconds in total). Performance of the blink detection task was high (mean hits = 98% , mean false alarms = 1.8%), demonstrating that these participants were attending to the stimuli. The adaptation blocks were followed immediately by a block of test trials. The post-adaptation test blocks differed from the baseline block in the following ways. After every fifth trial, an adaptation top-up was displayed for 4000 ms, which unlike in the full adaptation block, these top-ups would never blink. Secondly, this test block consisted of 100 gaze judgment trials and 20 top-ups. Hence, the entire block lasted 380 seconds. Then participants were adapted again in the same direction as before, followed by another test block. After this, participants were adapted to the opposite gaze direction and performed two further test blocks. Hence, for each adapted gaze direction, participants made 200 gaze judgments (40 per gaze stimulus). Participants were able to take rests after each test block. The entire testing session took approximately one hour.

Results and Discussion

The proportion of “straight” responses to each stimulus (gaze 17.5° to the left and right, 10° to the left and right, and straight ahead), in each adaptation condition (unadapted baseline, adapted left, adapted right) is illustrated in Figure 3, clearly

F3

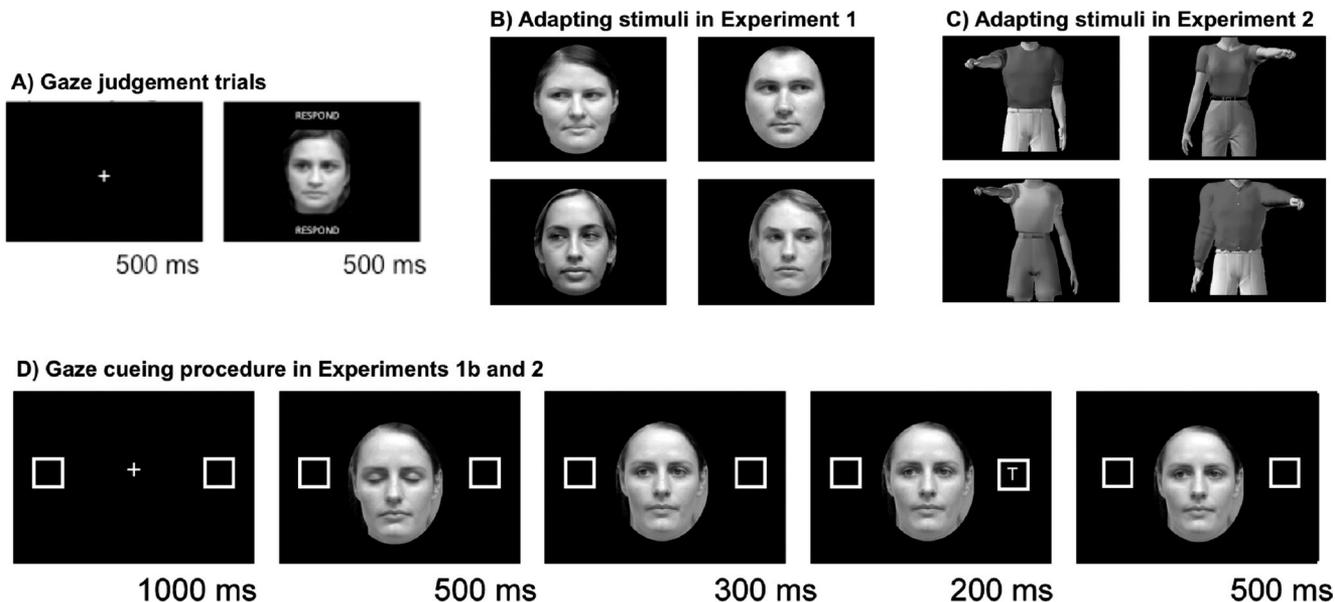


Figure 2. Examples of stimuli and trial procedures in this study. A) An example of a trial from the gaze judgment task. In this case, the eyes are deviated 17.5° to the left. A blank screen followed these displays for 2000 ms. B) Examples of the adapting stimuli, with gaze averted either 25° to the left or right. C) Examples of the pointing stimuli used as adapting stimuli in Experiment 2. D) The time course of a gaze cueing trial, as used in Experiments 1b and 2 (this example shows an “invalid” cue with the eyes are deviated by 10°).

demonstrating an effect of adaptation on gaze perception. Specifically, when adapted either to the left or right, participants were much more likely to judge gaze deviations 10° in the adapted direction as straight, replicating prior work (e.g. Jen-

kins et al., 2006). The arcsine transformed proportion data were submitted to a 3 (Adaptation condition) × 5 (gaze direction) analysis of variance (ANOVA), which revealed significant main effects of both factors, along with a significant interaction, all F 's > 6.2, p 's < .007.

To determine the effects of gaze adaptation on the proportion of “straight” responses assigned to each truly averted gaze stimulus, four contrasts were conducted. Significant effects of adaptation were evident for gaze stimuli averted 10° to the left, $t(14) = 4.03$, $p = .001$, with more frequent “straight” responses to these stimuli following adaptation to faces displaying 25° averted to the left ($M = 28.5\%$, $SD = 21.3$) than when the adapting stimulus was rightward gazing faces ($M = 11.7\%$, $SD = 11.2$). Similarly, adaptation was evident for the faces looking 10° to the right, $t(14) = 3.96$, $p = .001$, with more “straight” responses after rightward ($M = 44.8\%$, $SD = 24.2$) than leftward ($M = 24.2\%$, $SD = 17.8$) adaptation.

With test stimuli displaying 17.5° of gaze aversion, adaptation was much weaker. For leftward gazing faces, the effect was non-significant, $t(14) = 1.40$, $p = .183$ (Adapted $M = 2.2\%$, $SD = 2.5$; Unadapted $M = 1.8\%$, $SD = 4.5$). Significant adaptation was observed for rightward gazing faces, $t(14) = 2.27$, $p = .039$ (Adapted $M = 7.0\%$, $SD = 7.5$; Unadapted $M = 3.0\%$, $SD = 3.2$). This is an intriguing result, suggesting that reliable adaptation might be observable at this rather wide angle of gaze deviation. However, the absolute magnitudes (3% to 7%) are small in relation to the effects at 10°, so we simply note this relatively small effect with caution.

This experiment replicated the established findings (e.g. Jenkins et al., 2006; Seyama, 2006) demonstrating that repeated exposure to faces with averted gaze in one direction leads to a perceptual

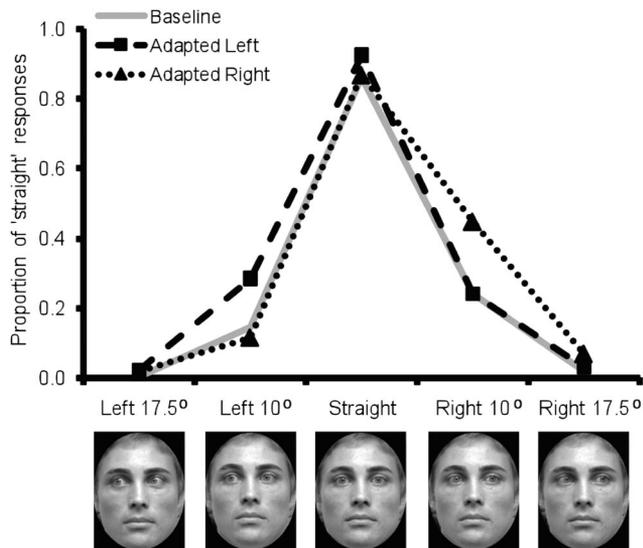


Figure 3. Mean proportion of “Straight” responses made to each of the five gaze directions under the three adaptation conditions in Experiment 1. The key feature of this pattern of data is that for the 10° gaze stimuli, the rate of erroneous “straight” responses vastly increases when they are looking in the same direction as the adapting stimuli, but not when the test stimulus is looking in the unadapted direction.

adaptation effect such that smaller angles of gaze in that direction are more often perceived as being directed straight at the observer than when the test stimulus is gazing in the opposite direction to the prior adapting stimuli.

Experiment 1b

If the gaze perception system is directly responsible for gaze cueing, then biasing the gaze perception system will also bias the attention system. Participants in this experiment were exposed to the same adapting stimuli as in Experiment 1. However, instead of judging the direction of gaze in the test faces, these test faces, gazing 17.5° or 10° to the left or right, served as nonpredictive spatial cues to attention in a speeded target discrimination task. The prediction is that these stimuli will produce strong shifts of attention in the observer when they oppose the direction to which the participant has been adapted—specifically for the more subtle 10° averted gaze cues.

Method

Participants

Thirty-two participants (mean age = 19.5 years, $SD = 2.0$; six were male) completed this experiment, in return for course credit or payment (\$10). Participants gave informed consent, but were naïve as to the aims of the study.

Stimuli

We employed the stimuli developed for use in Experiment 1a in this experiment, with some additions. For the cueing sections of the experiment, targets were the letter “T,” measuring $1.5\text{ cm} \times 1.5\text{ cm}$, and presented in white, upright or inverted, 6.0 cm from the centre of the screen, level with the fixation cross. Placeholders in the form of white squares, measuring $2.4\text{ cm high} \times 3.2\text{ cm wide}$, centred about the two target locations. As well as a white fixation cross, a larger ($1.2\text{ cm} \times 1.2\text{ cm}$) red cross was used as feedback on cueing trials in the event of an erroneous or slow response to the preceding trial (see Figure 2d).

Design

This experiment was divided into two parts. The first section was identical to the baseline block of judgment trials of Experiment 1a prior to any adaptation stimuli. This was included to ensure equivalent exposure to gazing faces across the two experiments. The second section differed from that of Experiment 1a. Here, participants responded to targets in an attentional cueing paradigm following adaptation to a particular gaze direction. Stimulus presentation and counterbalancing was managed in the same way as Experiment 1. Analysis focused primarily on averted gaze trials, with data from direct gaze cue trials analyzed separately. Hence, there were three within-subjects factors, each with two levels. The first was “Validity,” describing whether the gaze cue was looking in the direction of the target (Valid) or away from the target location (Invalid). Then, “Degrees” referred to whether the eyes were deviated 10° or 17.5° from straight ahead. Finally, the “Adaptation” factor determined whether the cue direction

matched the direction to which the participant had been adapted. So, a rightward gaze cue would be an “Adapted” gaze cue following adaptation to the 25° right gaze stimuli, but “Unadapted” when presented in a block following adaptation to the 25° left stimuli.

Because it is not possible to treat the data from the direct gaze cues in terms of “Validity,” we analyzed these separately, and coded them with respect to eventual target location. Hence, when the eyes looked straight ahead, the target could appear in the location that had been consistently looked at by the adapting stimuli, or away from that location. For these “Direct” gaze stimuli, there was therefore a single “Adaptation” factor that was submitted to analysis.

Procedure

Participants were introduced to two experimental tasks. The first was the gaze direction judgment task described in Experiment 1a. The participants only completed the baseline judgment task—they did not judge the direction of gazing faces after adaptation. Other aspects of the task, i.e. the adaptation blocks, blink detection and top-ups, were identical to Experiment 1a. In this sample, blink detection performance was also high, again showing that these participants were attending to the adapting gaze stimuli (mean hits = 99%, mean false alarms = 0.8%). After adaptation blocks, participants completed a gaze cueing task. Each of the trials in the gaze cueing task began with the presentation of a fixation cross, flanked by two placeholder boxes for 1000 ms. Next, a face with closed eyes appeared in the centre of the screen. After 500 ms, the eyes appeared, looking in one of the five gaze directions. After a cue-target stimulus onset asynchrony of 300 ms, the target appeared in one of the placeholder boxes for 200 ms. This was either an upright or inverted letter “T.” Participants were told that the gaze of the face was uninformative as to the target location or identity and that they should ignore it while making quick and accurate target discrimination by pressing the “h” key on the keyboard with their first finger if the T was upright, and hitting spacebar with their thumb if the T was inverted. The face remained on the screen for an additional 500 ms. Finally, if the participants responded correctly, a white fixation replaced the face for 500 ms, or a larger, red cross if an incorrect or slow ($>1000\text{ ms}$) response was made.

An experimental session proceeded as follows. Participants first completed 20 practice trials of the gaze judgment task, then 20 of the gaze cueing task. Next, they completed 120 baseline gaze judgment trials and then the first of four adaptation blocks that were identical to that of Experiment 1. A gaze cueing block followed each adaptation block. This contained top-up adaptation stimuli after every fifth gaze cueing trial. Each of the four gaze cueing blocks lasted 380 seconds, identical to the duration of the post-adaptation gaze judgment trials in Experiment 1. Hence, over the session, participants were exposed to 400 gaze cueing trials, with 40 trials per each critical condition in the central $2 \times 2 \times 2$ design, plus a total of 80 straight gaze trials. As the gaze direction did not predict target location, the proportion of left and right targets was 50/50 for each of the five gaze directions. Each experimental session took approximately one hour.

Results

Participants made errors or failed to respond within 1000 ms of target onset in a total of 8.3% of trials (see Table 1). The arcsine transformed error rates were submitted to a 2 (Degrees; 17.5 vs. 10) × 2 (Adaptation; Gaze cue in adapted direction vs. Gaze cue in unadapted direction) × 2 (Validity; Eyes look at target vs. Eyes look away from target location). No significant effects were detected, all $F_s < 1.52$, $p_s > .22$.

The mean reaction times of each participant’s correct responses in each condition were submitted to the same analysis as above (see Figure 4). Here, classical attentional facilitation for targets in valid locations was observed with a significant effect of “Validity,” $F(1, 31) = 27.8$, $MSe = 328$, $p < .001$, $\eta_p^2 = .47$, with quicker reaction times (RTs) to valid targets (438 ms) than to invalid targets (450 ms). The “Validity” × “Adaptation” interaction was significant, $F(1, 31) = 6.94$, $MSe = 151$, $p < .013$, $\eta_p^2 = .18$, because when the cue direction was in the same direction as the preceding adapting stimuli, cueing was weaker (8 ms) than when the cues were opposite to the adapted direction (16 ms). No other effects approached significance, $F_s < 2.5$, $p_s > .12$. We specifically predicted that the impact of adaptation on attention would be strongest when the cue subtended only 10° in gaze deviation. Thus we conducted two further ANOVAs to investigate the impact of adaptation on the strength of gaze cueing elicited by 10° and 17.5° gaze cues separately.

Hence, a 2 (Validity) × 2 (Adaptation) ANOVA was conducted on the 17.5° data in isolation. Here, “Validity” was significant, $F(1, 31) = 23.2$, $MSe = 323$, $p < .001$, $\eta_p^2 = .43$, however the interaction between “Validity” and “Adaptation” did not approach significance, $F(1, 31) = 1.07$, $MSe = 178$, $p = .31$, $\eta_p^2 = .17$. Both cues in the adapted, $t(31) = 3.27$, $p = .003$ (13 ms cueing) and in the unadapted, $t(31) = 4.46$, $p < .001$ (18 ms cueing effect) directions produced reliable gaze cueing effects.

The same analysis was performed on the data from the 10° gaze cues. As well as a significant cueing effect, $F(1, 31) = 7.67$, $MSe = 306$, $p = .009$, $\eta_p^2 = .20$, the interaction was significant, $F(1, 31) = 6.52$, $MSe = 178$, $p = .016$, $\eta_p^2 = .174$. Follow-up contrasts confirmed that 10° gaze cues in the adapted direction were ineffective cues to attention, $t(31) = .74$, $p = .47$ (2 ms cueing effect), while cues in the unadapted direction produced significant gaze cueing effects, $t(31) = 3.88$, $p < .001$ (14 ms cueing effect). Overall, these results were in line with the prediction that

adaptation to averted gaze in one direction would lead to weakened gaze cueing being elicited by gaze cues in that direction, but normal levels of cueing from gaze cues in the unadapted direction.

One final contrast investigated the possibility that following adaptation, even the direct gaze cues, presented on 20% of trials, could produce a shift of attention away from the direction of adaptation, as if they were perceived as looking away from the adapting direction. Participants responded slightly faster (445 ms) to targets appearing on the opposite location to which the adapting stimuli were looking than targets appearing in the location looked at by the adapting stimuli (448 ms), but this difference did not approach significance, $t(31) = .77$, $p = .45$. This is an important null result, because it shows that the adaptation procedure did not result in a generalized attentional bias away from the adapted direction. This, along with the equivalent cueing effects shown with 17.5° cues in the adapted and unadapted directions, suggests that the differences found at 10° are due to the specific biasing of the gaze perception system. Therefore, the data from this experiment provide very strong evidence for a direct role of gaze direction representations being the driving force for gaze cueing of attention.

Discussion

This experiment provides strong support for the notion that adaptation to gaze direction has an impact on gaze-cueing as well as explicit gaze perception. Adapting to a gaze stimulus that looks 25° to the left or right results in reduced gaze cueing in that direction. This is demonstrated by showing a null effect of gaze cues that subtend 10° in the adapted direction relative to the unadapted direction. As such, this is indicative of the contribution of a direct link between the gaze perception system to the emergence of joint attention behaviors.

It is possible to forward an alternative account for our data. Can we be sure that adaptation to gaze direction modulates the sensitivity of the attention system to gaze cues alone? Previous work suggests that we can have confidence in this assertion. Only judgments of gaze direction are affected by gaze adaptation, while general spatial perception is unaffected (Jenkins et al. 2006). Further, arrows do not produce adaptation effects on gaze perception (Seyama, 2006). It is therefore difficult to imagine that adapting to gaze direction would affect attentional cueing in general given the prior demonstration of the gaze-specificity of the adaptation effect. It might also be argued that the adaptation procedure biased attention at an even more coarse level than considered above. The participant views 32 (in effect) gaze

Table 1
Mean Reaction Times (in ms) and Percent Errors for Each Condition (SD in Parentheses) for the Gaze Cueing Tasks in Experiment 1b and 2

	17.5° averted gaze				10° averted gaze				Direct gaze	
	Unadapted		Adapted		Unadapted		Adapted		Unadapted	Adapted
	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Neutral	Neutral
Experiment 1b										
RT	438 (50)	456 (58)	437 (52)	450 (54)	437 (52)	451 (54)	442 (53)	444 (52)	445 (49)	448 (52)
Errors	7.7 (7.5)	8.5 (7.8)	9.5 (8.5)	9.1 (8.4)	7.5 (6.3)	8.0 (7.0)	7.9 (7.7)	8.4 (6.6)	8.4 (7.8)	8.0 (7.0)
Experiment 2										
RT	407 (42)	415 (42)	402 (39)	410 (37)	400 (39)	412 (43)	400 (35)	410 (38)	413 (40)	408 (41)
Errors	7.4 (4.6)	8.1 (5.9)	7.2 (5.8)	9.1 (6.3)	7.1 (5.3)	7.6 (4.8)	8.4 (5.7)	8.6 (6.1)	7.8 (6.4)	9.3 (5.9)

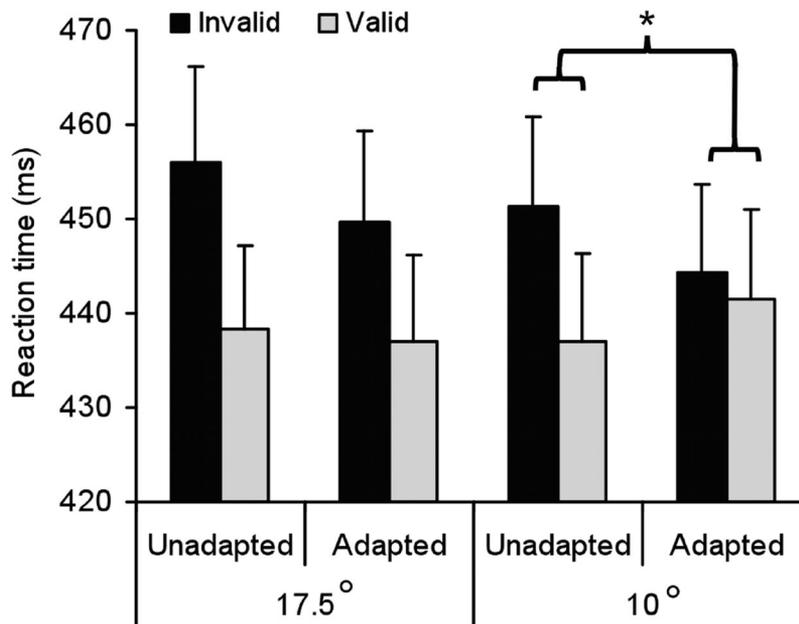


Figure 4. Mean reaction times (bars denote standard error) for each condition for the gaze cueing task in Experiment 1b. Gaze cueing emerges in all conditions (quicker RTs for valid as compared with invalid trials), except for the 10° gaze cues when looking in the adapted direction, where it is significantly weaker than the 10° in the unadapted direction. (* $p < .05$).

cues in one direction (e.g. left) for a total of 128 seconds. This presumably causes a consistent shift of attention to the left over the course of the block in the direction of perceived gaze. The constant orienting in one direction caused by the repetitive gaze cues might have instigated some form of sustained inhibition of return (“IOR”, e.g. Frischen & Tipper, 2004). In search, returning to previously inspected regions of space that contain no useful information is wasteful, so inhibition of return biases against this (Klein, 2000). The adaptation procedure repeatedly causes orienting to an uninteresting area of space, so could potentially cause strong inhibition of that region for the ensuing cueing trials. Indeed, although IOR is generally conceived of as a short term phenomenon (from 300 to 3000 ms post cue; Samuel & Kat, 2003), experimental reports have shown long term IOR (Tipper, Grison, & Kessler, 2003). Early reports of IOR dismissed the origin of the effect as habituation of the orienting response in favor of the novelty preference biasing search hypothesis. However, recent conceptualizations have reinvigorated this notion (Dukewich, 2009). While this speculative account might help explain the pattern of data found with our 10° conditions, this argument would predict exactly the same pattern with the 17.5° conditions, and also an overall slowing of responses to targets in the adapted location relative to the adapted location with direct/neutral gaze cues. Because adaptation had no reliable effect at 17.5° or with straight gaze cues, an overall spatial bias in attention appears unlikely to account for the data pattern in Experiment 1b.

Nevertheless, cueing of spatial attention can produce unexpected effects, and it is not clear how the attentional orienting system might respond under the unusual conditions we present it with here. For example, while the null effect of adaptation on target discrimination following direct gaze cues supports our central conclusion, a null effect is not necessarily strong support, and

furthermore, performance in response to “neutral” cues is historically fraught with difficulties for interpretation. Therefore, in Experiment 2, we seek evidence from another source to demonstrate that repeated exposure to an attentional cue is unlikely to account for the findings of Experiment 1b.

Experiment 2

The primary aim of this experiment was to discriminate between two plausible explanations for the pattern of data shown in Experiment 1b. The first is that the perceptual effects of gaze adaptation directly influence the spatial attention system responsible for the gaze cueing effect. The alternative account, tested here, is that the *attentional* effects of a repeated directional cue give rise to the differences in the potency of gaze cues following adaptation.

One way to investigate this issue is to replace the adapting stimulus with a non-gaze directional stimulus that is at least as potent an attentional cue as averted gaze, but that can also be presented as deviating 25° from straight ahead. We decided to use pointing stimuli (arm and finger of a human-looking avatar torso) as adapting stimuli (see Figure 2c). After confirming that these stimuli produce reliable cueing effects,¹ we implemented the same experimental design as Experiment 1b, but replacing the gaze

En1

¹ We presented 14 participants with small (2.5 cm × 5 cm) versions of the pointing stimuli in a brief cueing paradigm (40 trials per condition) with spatial and temporal parameters identical to the gaze cueing paradigm used in Experiments 1b and 2. Significant cueing effects were confirmed, $t(13) = 7.70, p < .001$ (Valid RT = 390 ms; Invalid RT = 433 ms). We can therefore assume that any attentional effects of the adapting stimuli in Experiment 2 were at least as strong as in Experiment 1b.

adaptation stimuli with these new pointing stimuli. These stimuli work very well as a comparison stimulus to gaze stimuli as they are perceived as biological stimuli, produce strong attentional effects, but yet are physically very different to the gaze stimuli. It is very important to note here that the hypothesis that is being tested with this experiment is that the data from Experiment 1b could be due the adaptation procedure producing an “attentional-adaptation” effect. Therefore whether or not these pointing stimuli produce any form of *perceptual* adaptation effect is irrelevant to the present question. As they elicit spatial orienting effects, we can test whether repeatedly stimulating the attention system with a *non-gaze* cue to attention can subsequently modulate gaze-cueing effects, or not.

Method

Participants

Thirty-five participants completed the study (mean age = 20.0 years, $SD = 2.9$ years, four were male). All participants provided informed consent and were naïve to the aims of the study.

Stimuli

In addition to the stimuli used in Experiment 1, we produced a set of “pointing” avatars from Poser 5.0 (Curious Labs., Inc.). These computer generated torso sections (from waist to neck) of two males and two females were manipulated to point, with arm and forefinger extended, 25° to the left or right with the left or right arm, respectively. The angle was calculated as the deviation from a straight point towards the observer. The nonactive arm would rest vertically by the side of the torso (and for the “blink” trials, both arms would be relaxed at the side of the torso, as a proxy for the “eyes closed” stimuli from Experiment 1). The torsos measured approximately 5 cm (shoulder width) by 10 cm, and the pointing arms extended an additional 4 cm away from the centre of the screen (see Figure 2).

Design and Procedure

The structure of the experiment was identical to that of Experiment 1b, with the exception of the “Adaptation” blocks. In this experiment, participants viewed a constant stream of avatars pointing in the same direction (left or right). During these blocks, the participants’ task was to detect those occasions when the arm of the avatar moved to its side and back again. Performance on this task was again close to perfect (mean hits = 97%, mean false alarms = 0.4% of trials). The gaze perception baseline task, and the post-adaptation gaze-cueing sections were identical to Experiment 1b.

Results

To investigate the gaze cueing effects that followed adaptation to pointing gestures, we conducted the same analysis as in Experiment 1b. Errors and slow (>1000 ms) responses were made on 7.9% of trials. The arcsine transformed error rates were submitted to a 2 (Degrees; 17.5 vs. 10) \times 2 (Adaptation; Gaze cue in adapted direction vs. Gaze cue in unadapted direction) \times 2 (Validity; Eyes

look at target vs. Eyes look away from target location). No significant effects were detected, all $F_s < 2.6$, $p_s > .11$. The mean RTs on correct trials were submitted to the same analysis (see Table 1). This revealed a significant cueing effect through the main effect of “Validity,” $F(1, 34) = 6.52$, $MSe = 210$, $p < .001$, $\eta_p^2 = .466$ (RT for valid trials = 402 ms, RT for invalid trials = 412 ms). The only other effect to reach significance was “Adaptation” due to generally faster RTs when the target appeared on the adapted side of the screen (406 ms) than the unadapted side (409 ms), $F(1, 34) = 4.82$, $MSe = 133$, $p = .035$, $\eta_p^2 = .124$. The main effect for “Degrees” hinted towards a trend, $F(1, 34) = 2.83$, $MSe = 166$, $p = .10$, $\eta_p^2 = .078$, but all the critical interactions with adaptation, degrees and validity were far from reaching statistical significance, $F_s < 1.7$, $p_s > .21$.

Discussion

In this experiment, gaze cues had the standard effect on attentional orienting. However, adapting to pointing cues had no effect whatsoever on the magnitude of this effect. This is in stark contrast to the findings of Experiment 1b, where adaptation to gaze direction did modulate gaze cueing in a particular pattern. This strongly suggests that repeated exposure to a directional cue *per se* does not necessarily lead to a modulation of attentional orienting elicited by gaze cues. This supports the assertion that the effects of gaze adaptation on gaze cueing in Experiment 1b are in fact due to the perceptual effects of gaze adaptation stimuli, not the concomitant attention orienting effect that is presumed to occur during the adaptation procedure.

General Discussion

This study was designed to investigate the role of the gaze perception system in the generation of the automatic attention shifts that enable the establishment of joint attention. As a cornerstone of important social interactions, it is a fundamental goal of the study of social cognition to identify and describe the mechanisms and processes that are involved in social attention. Establishing whether gaze cueing is a unique form of orienting—that the attention system treats directional gaze cues as special stimuli due to their importance in the social context—has been a focus of several previous studies (e.g. Friesen et al., 2004; Tipples, 2008).

However, this quest has been problematic because gaze cueing has several unexpected properties if eyes are indeed a special attentional stimulus. One important observation is that there are few behavioral differences between the control that gaze and arrow cues have over attention. In general, whereas eyes do dominate the attention system as a prioritized stimulus, this is perhaps limited to their enhanced ability to capture the attention of the observer compared with other directional cues (cf. Birmingham, Bischof, & Kingstone, 2009). That such stimuli have privileged access to the system does not mean that the decoding of that stimulus once in the system is in any way unique.

Another way to approach the question of the origin of the gaze cueing effect is to ask what representations the attention system is acting upon to produce a shift of attention. There are two distinct possibilities. Firstly, the attention system could derive directional information from all types of cues in the environment whatever the underlying form in the same way. If this is the case, then the

specific mechanisms that underlie gaze perception need not be involved at any stage since the attention system only requires cue-general low level information. The second possibility is that the attention system acts on the output from a specialized mechanism dedicated to discrimination of gaze direction. In this study we were able, by manipulating the output of the gaze perception system through utilization of the gaze adaptation paradigm, to lend strong support to the second possibility.

Adaptation of the gaze perception system modulated gaze cueing effects (Experiment 1b). We conclude, therefore, that attention shifts following presentation of an averted eye gaze cue indeed rely on the output from the gaze perception system and not on a generalized derivation of directional information that could be applied to any stimulus. Specifically, relatively weak gaze cues, subtending 10° of aversion, were ineffective at biasing attention to the looked-at direction when a series of adapting stimuli had been previously presented looking 25° in that direction. Conversely, 10° gaze cues were effective cues when looking in the opposite direction to the adapting stimuli. Stronger gaze cues, subtending 17.5° were relatively unaffected by the adaptation procedure, suggesting that this 17.5° gaze signal was strong enough to trigger a shift of attention in that direction in spite of adaptation. Further support for relative independence of a gaze cueing system from other forms of orienting was evident from Experiment 2, which showed that gaze cueing is insensitive to adaptation of the attention system more generally—repeated exposure to pointing stimuli did not bias subsequent gaze cueing effects.

Therefore, we believe these data provide evidence that adapting to gaze stimuli biases the attention shifts generated by gaze cues in a highly specific manner predicted by recent functional accounts of gaze perception (Calder et al., 2007; 2008; Nummenmaa & Calder, 2009). This strongly suggests a direct causal link between the gaze perception system and the attentional mechanisms responsible for generating joint attention episodes. In other words, the signals that the attention system receives prior to executing a gaze cued shift of attention are based on the aggregate output from the multichannel coding (left, right, and straight) of cells sensitive to gaze direction, rather than from a system operating at a lower, more generalized level that can act on any given directional signal (e.g. a pointing finger or arrow).

At this point it may be useful to reiterate that we feel that our data lend support to the notion of a *contribution* by a gaze perception module to gaze cueing; we do not contend that other systems are not involved or could under some circumstances potentiate orienting to gaze direction. For example, one interesting avenue for future work to further pick apart the mechanisms underlying gaze cueing would be to investigate whether explicit gaze perception is necessary for these effects to emerge. Recent work has shown that briefly presented, masked gaze cues can produce reliable (but of course relatively weak) gaze cueing effects on attention despite participants being unable to report the direction of the cue (Sato, Okada, & Toichi, 2007). Since gaze cueing does not always require conscious awareness, it would be interesting to examine the effects reported in this paper with masked gaze cues. If, for example, gaze adaptation has no effect on subliminal gaze cueing, then it might suggest that visual processes that operate prior to the engagement of *specialized* gaze perception mechanisms are responsible for the effects reported by Sato et al.

The previous paragraph considers the role of visual processing prior to the calculation of gaze direction by a specialized gaze perception system. However, higher-level, top-down signals can certainly play a role in determining the magnitude of gaze cueing. Take, for example, work by Ristic and Kingstone (2005), who showed that an ambiguous stimulus only cued attention when participants were invited to perceive it as a gazing face, but not when it was described as a car. Furthermore, Teufel, Alexis, Clayton, and Davis (2010) have shown that gaze cueing is stronger when elicited by an observed head turn when the observer is led to believe that the swimming goggles the model is wearing are see-through than when they are assumed to be opaque (see also Nuku & Bekkering, 2008). Hence, it is abundantly clear that there are multiple sources of information that can determine the strength of a social orienting response. Our present data provide support to the idea that one important source is likely to be the aggregate output from the gaze perception system theorized by Baron-Cohen (1995) and Perrett et al. (1992) among others and functionally described by Calder et al. (2008).

Finally, it is noteworthy that inferences from fMRI (Calder et al., 2007) and monkey neurophysiology (Shepherd, Klein, Deaner, & Platt, 2009) suggest that the anterior STS is not the only region with gaze sensitive cells, because the IPL appears to contain cells with similar response properties to the anterior STS cells. The STS remains one of the primary regions of exploration for researchers interested in social cognition (Allison et al., 2000; Nummenmaa & Calder, 2009) and the role of the IPL in such processes is less well known. It is nevertheless tempting to speculate that cells in the IPL may be the target for afferent signals from the aSTS encoding gaze direction to regions controlling the distribution of attention across space. Clearly a more comprehensive description of the mechanisms underlying gaze triggered orienting is needed to not only answer questions about how the brain organizes social behavior, but also to approach a deeper understanding of where in the system problems in joint attention emerge in developmental disorders and social phobias.

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