Report

Social Cognition Modulates the Sensory Coding of Observed Gaze Direction

Christoph Teufel,[1,*] Dean M. Alexis,[1] Helena Todd,[1] Adam J. Lawrance-Owen,[1] Nicola S. Clayton,[1] and Greg Davis[1,*]
[1]Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK

Summary

Gaze direction is an important social signal in both human and nonhuman primates, providing information about conspecifics' attention, interests, and intentions [1–4]. Single-unit recordings in macaques have revealed neurons selective for others' specific gaze direction [5, 6]. A parallel functional organization in the human brain is indicated by gaze-adaptation experiments, in which systematic distortions in gaze perception following prolonged exposure to static face images reveal dynamic interactions in local cortical circuitry [7, 8]. However, our understanding of the influence of high-level social cognition on these processes in monkeys and humans is still rudimentary. Here we show that the attribution of a mental state to another person determines the way in which the human brain codes observed gaze direction. Specifically, we convinced observers that prerecorded video sequences of an experimenter gazing left or right were a live video link to an adjacent room. The experimenter wore mirrored goggles that observers believed were either transparent such that the person could see, or opaque such that the person could not see. The effects of adaptation were enhanced under the former condition relative to the latter, indicating that high-level sociocognitive processes shape and modulate sensory coding of observed gaze direction.

Results and Discussion

The sensitivity of many neurons decreases in response to prolonged stimulation, and such adaptation has proven a powerful tool for relating neurophysiology to perception [9, 10]. Adaptation is frequently evident as aftereffects, specific and measurable distortions of perception that reflect reduced contributions of adapted processes. Initially only reported for basic aspects of vision, recent studies have demonstrated aftereffects for more sophisticated processes underpinning perception of facial identity and gestures [11–13]. In one example, the effects of adaptation have been exploited to study the human gaze-processing system, demonstrating that after prolonged exposure to a person looking in a particular direction, subsequent gaze-direction judgment is biased in the opposite direction [7, 8, 14–17]: adaptation to a leftward-gazing face distorts estimation of subsequently presented gaze direction rightward, and the converse pattern obtains following adaptation to a rightward-gazing face. Such psychophysical assessments of gaze-direction aftereffects indicate the existence of distinct populations of neurons coding specifically

for different observed gaze directions. Moreover, recent experiments combining adaptation and functional magnetic resonance imaging (fMRI) have localized the blood oxygen level-dependent (BOLD) signal correlates of these aftereffects in the human superior temporal sulcus (STS) [7], lending support to the notion that the gaze-adaptation paradigm to a certain extent constitutes a noninvasive human analog to the single-unit recording employed by Perrett and colleagues in the macaque brain [5, 6].
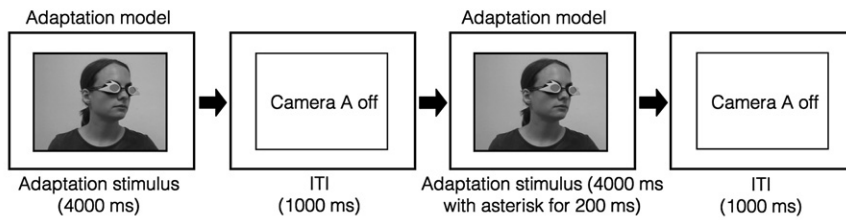
Here, we do not revisit issues concerning the anatomical loci associated with these adaptable processes but rather seek to describe the environmental features that they encode. Several influential reports have suggested that STS neurons code where another individual is directing their visual attention—suggesting that they may play a role in the processing of others' mental states rather than simply coding the physical features of eye or head orientation [5, 18]. However, previous studies have stopped short of directly manipulating the observers' belief of whether or not a face stimulus can see, an experiment that could directly show that input from mental-state attribution is incorporated into the gaze-processing system. According to this view, such a manipulation should exert a powerful modulatory effect on adaptation to gaze (and hence on the magnitude of the gaze-direction aftereffect).

In order to guarantee the participants' attribution of mental states to the face stimuli, we employed an elaborate deception procedure, convincing observers that prerecorded videos showing the faces of two experimenters on a computer screen were a live video link to two adjoining rooms. The observers thus believed they were interacting with two real people in the experiment. They were first adapted to the face of one experimenter (adaptation model) looking into a particular direction and subsequently had to judge a second experimenter's gaze direction (test model) (Figure 1). To directly manipulate the mental state that the observers attributed to the adaptation model, the model wore either a blue or a yellow pair of goggles, both with highly mirrored lenses such that it was impossible to see the eyes of the wearer. From the perspective of the person wearing the goggles, however, one pair was transparent and the other was completely opaque. Prior to the experiment, half of the participants experienced that they could see through the yellow pair of goggles but not through the blue pair, and vice versa for the other half. While watching the video clips, they therefore believed that when wearing one pair of goggles, the adaptation model could see (seeing condition), whereas with the other pair, the model was not able to see (nonseeing condition). Participants were thus encouraged to attribute a specific sensory capability to the adaptation model (but no mental contents). After this adaptation phase, the observers' acuity in judging the gaze direction of the test model was assessed.

Observers' gaze-direction judgments differed following adaptation to leftward versus to rightward gaze, indicating an influence of adaptation on gaze processing (Figure 2A). Crucially, this effect was only present when observers believed that the model was wearing transparent goggles and could see, but was absent when they believed that the model was wearing opaque goggles and could not see. A 2 × 2 × 3

*Correspondence: crt35@cam.ac.uk (C.T.), gjd1000@cam.ac.uk (G.D.)

Adaptation Phase

Adaptation model

Adaptation stimulus
(4000 ms)

Camera A off

ITI
(1000 ms)

Adaptation model

Adaptation stimulus (4000 ms
with asterisk for 200 ms)

Camera A off

ITI
(1000 ms)

Postadaptation Acuity Test

Adaptation model

Top-up adaptation
stimulus (4000 ms)

Camera A off

Signal Screen
(500 ms)

Test model

Test Stimulus
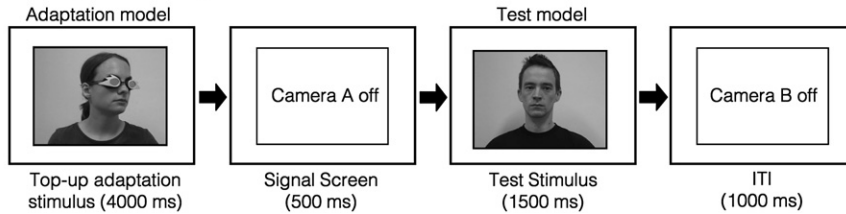(1500 ms)

Camera B off

ITI
(1000 ms)

Figure 1. Schematic View of the Experimental Procedure

All examples show adaptation to rightward gaze by the adaptation model. As a result of an elaborate deception procedure, observers believed they were interacting with two real people connected to the screen via a live video link during the experiment. Observers were first adapted to the face of the adaptation model with the head turned 25° to look either to the left or the right (adaptation phase) and subsequently had to judge the second experimenter's gaze direction by pressing a response button to indicate rightward, straight, or leftward gaze (postadaptation acuity test). Three categories of test stimuli were used, showing the test model with the head pointing straight ahead and the eyes directed 5° to the left, straight ahead, or 5° to the right. Top-up adaptation stimuli were used to maintain adaptation during the test. The signals on the screen during the intertrial intervals (ITI) were presented in order to maintain the impression that the prerecorded video clips were a live video link to two adjoining rooms. All observers participated in the seeing and the nonseeing condition, with half of them believing that the adaptation model was able to see through the yellow goggles but not through the blue ones, and half believing the reverse. Within each condition, observers' gaze-direction judgments were tested after adaptation to both leftward and rightward gaze of the adaptation model in two separate sessions. Note that all observers watched the same set of video clips. Across observers, the only manipulation that varied consistently was the observers' belief concerning the ability of the adaptation model to see through the goggles.

repeated-measures analysis of variance (ANOVA) (condition [seeing versus nonseeing] × adaptation side [left versus right] × test stimulus [5° left, straight, or 5° right]) confirmed these impressions. There was a significant main effect of adaptation side ($F_{(1,19)} = 7.61$, $p < 0.05$) and test stimulus ($F_{(1,19)} = 2096.53$, $p < 0.001$) and no effect of condition ($F < 1$). Importantly, however, there was a significant adaptation side × condition interaction ($F_{(1,19)} = 5.90$, $p < 0.05$), indicating that the effect of adaptation was influenced by the observers' belief concerning the adaptation model's ability to see. All other interactions were not significant.

To reveal the source of the interaction, we analyzed the seeing and nonseeing data separately via 2 × 3 repeated-measures ANOVAs. As expected, both analyses yielded significant main effects of test stimulus (both $F_{(1,19)}$s > 1015.96, $p < 0.001$) and no interaction term (both $Fs < 1$). Crucially, however, the analysis of the seeing condition yielded a main effect of adaptation side ($F_{(1,19)} = 17.59$, $p < 0.001$), whereas this was not the case for the nonseeing condition ($F_{(1,19)} = 1.31$, NS). In line with previous work, we also conducted planned Wilcoxon signed-rank tests to assess adaptation at each level of the test stimulus factor. For the seeing condition, significant influences of adaptation side were observed for test stimuli facing 5° right ($Z = 2.46$, $p < 0.05$) and straight ahead ($Z = 2.23$, $p < 0.05$), but not for test stimuli facing 5° left ($Z = 0.92$, NS). In the nonseeing condition, no effect of adaptation side was observed in any of the three categories of test stimuli (all $Zs < 1.03$, NS).

Experiment 1 thus provided initial evidence suggesting that gaze processing is influenced by an observer's attribution of the mental state "seeing," as opposed to "nonseeing," to another person. This conclusion has one caveat. Observers' attention to the display as a whole had been maintained by a "sham" task during the adaptation phase—two asterisks briefly flashed up to the left and right of the model's face, and participants had to respond as quickly as possible by pressing a button. However, the locations of these asterisks did not permit us measuring whether attention was allocated

equally to the adaptation model's face in the seeing versus the nonseeing conditions. Accordingly, though there was no a priori reason to assume that this had happened, it remained possible to account for the results of experiment 1 by positing that the participants allocated more attention to a "seeing" than to a "nonseeing" face.

In order to address this issue, we conducted a second experiment. The key innovation in experiment 2 was that in half of the trials during the adaptation phase, an asterisk briefly flashed up in one of twelve different locations distributed over the eye region of the adaptation model, rather than to either side of the face. The task for the observers was to indicate the appearance of the asterisk as quickly as possible by a button press. The response times were used as a refined measure of attention allocated to the face of the adaptation model. We also used a novel set of videos showing a new adaptation model and a new test model. This allowed us to additionally address why no aftereffect was observed in response to test faces gazing 5° left in the seeing condition in experiment 1. If this aberrant result reflected a new lateralized component in gaze processing specific to mental-state attribution, then it should arise again with these new stimuli. Conversely, if the same result did not arise, we could dismiss the result in experiment 1 as simply a reflection of subtle unintended biases in our test stimuli.

The results of experiment 2 showed a pattern similar to those of the previous experiment (Figure 2B). An ANOVA identical to the primary analysis of experiment 1 yielded significant main effects of adaptation side ($F_{(1,15)} = 29.29$, $p < 0.001$) and test stimulus ($F_{(1,15)} = 2811.29$, $p < 0.001$), but again no effect for condition ($F_{(1,15)} < 1$, NS). Crucially, as in experiment 1, there was also a significant adaptation side × condition interaction ($F_{(1,15)} = 5.91$, $p < 0.05$). No other interactions were significant.

As expected, separate analyses of the seeing and the nonseeing condition as in experiment 1 yielded main effects of test stimulus (both $F_{(1,15)}$s > 1499.43, $p < 0.001$) but no significant interaction (both $Fs < 1$). The factor adaptation side
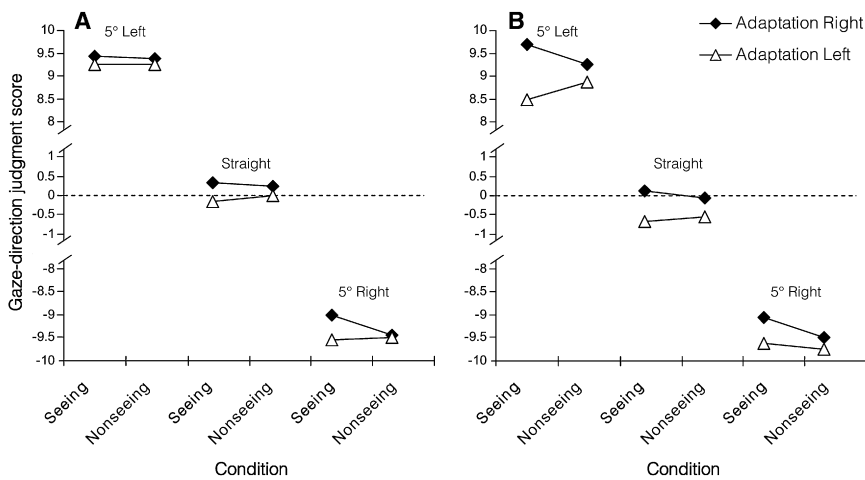
Figure 2. Mean Combined Scores of Gaze-Direction Judgment for the Test Stimuli 5° Left, Straight, and 5° Right in the Seeing and the Nonseeing Condition

A positive value indicates a bias to judge gaze direction as left; a negative value indicates a bias to the right. Note that the y axis is broken.
(A) Experiment 1.
(B) Experiment 2.

showed a significant main effect for both the seeing ($F_{(1,15)} > 26.29$, $p < 0.001$) and the nonseeing condition ($F_{(1,15)} > 8.05$, $p < 0.05$). For the seeing condition, significant influences of adaptation side were observed for test stimuli facing 5° right ($Z = 2.12$, $p < 0.05$), straight ahead ($Z = 2.48$, $p < 0.05$), and 5° left ($Z = 2.53$, $p < 0.05$). In contrast, for the nonseeing condition, effects of adaptation side again did not reach significance for test stimuli gazing left or right (both $Zs < 1.3$, NS), though they did for faces gazing straight ahead ($Z = 2.13$, $p < 0.05$).

The reliable aftereffect in this last case was the only one of six nonseeing conditions across our two studies to reach significance. One possibility is that the greater insistence in experiment 2 on attending to the face had permitted a small effect to arise in that study. However, given that the aftereffect was still significant only in one of three nonseeing conditions, it appears that gaze adaptation in the absence of the observer attributing the mental state "seeing" to a face is minimal. Moreover, this absence of an effect did not reflect reduced allocation of spatial attention to the eye region of the face stimulus in the nonseeing versus the seeing condition. Response times to asterisks presented during the adaptation phase on the face stimulus did not differ significantly for the seeing and the nonseeing condition ($t(15) = 1.19$, NS).

Taken together, the results of the two experiments indicate that the coding of gaze during adaptation must have been differently influenced by the attribution of a "seeing" or a "nonseeing" mental state to the adaptation model. During adaptation, the eyes of the model were never visible, and the subsequent aftereffects might therefore have reflected coding of the model's eye direction inferred from head orientation rather than coding of head orientation per se. In either case, the finding that adaptation to head orientation transferred to perception of eye direction implicates mechanisms that exploit both sources of orientation information, paralleling findings in the primate brain [5, 6]. Although eye direction is an important social cue of where others are looking, the availability of this information diminishes dramatically with increasing distance between the observed individual and the observer. Considering these ecological constraints, a system that exploits various sources might be necessary to yield reliable estimates of where others are looking.

A particular advantage of our method is that physical differences between the stimuli cannot explain our results; the only variable that differed consistently across observers between seeing and nonseeing conditions was observers' belief with respect to the adaptation model's ability to see. Previous studies provide some indication that high-level social cognition and face categorization can influence the allocation of spatial attention in response to a gaze cue [19, 20]. However, our findings demonstrate for the first time that the sensory coding of a gaze cue's physical characteristics can be top-down modulated by mental-state attribution.

At first glance, the adaptive advantage of such a sophisticated system might not be apparent. However, recent studies in object recognition suggest that, in processing nonsocial information, the brain exploits both feedforward and feedback informational flow between areas implicated in low-level perception and areas responsible for higher-order belief formation when dealing with complex and ambiguous information (e.g., [21–23]). Similarly, within the social domain, top-down modulation of social perception by mental-state attribution might be necessary to guarantee optimal performance of the basic gaze-processing system in natural scenes. In our experimental design, physically identical-looking gaze cues had radically different meanings, signaling that the model either could or could not see. In everyday life, similar situations might occur in complex social settings in which various potential targets and barriers between looker and target are the norm. In order to disambiguate these situations, a gaze-processing system as sophisticated as demonstrated in the current study might be necessary.

From a neuropsychological perspective, the most important interpretative issue arising from the current results concerns the level at which an observer's belief about another person's ability to see influences the neural representation of where others are looking. Our psychophysical procedure does not speak further to the localization of such effects in the brain. In principle, they could arises entirely in the STS; however, given the sophistication of the sociocognitive manipulation that influenced gaze coding in our studies, it would seem certain that areas implicated in mental-state attribution such as the medial prefrontal cortex and the temporoparietal junction [24–27] are necessary for the reported subtleties of gaze processing. Both regions are closely associated with the STS. Accordingly, it would appear that our effects reflect top-down modulation of gaze processing in the STS by prefrontal and temporoparietal regions recruited by the attribution of mental states. Specifically, this system appears to control the depth of gaze processing.

In summary, our findings indicate a bidirectional relationship between gaze processing and the system responsible for mental-state attribution. Previous studies have demonstrated that observed gaze direction can be used to infer another person's mental states such as attention (e.g., [28, 29]). Here we demonstrate that beliefs about another person's ability to

see (and therefore to attend) in turn have strong top-down effects on gaze processing. With respect to the particular case of human observers, this finding provides clear evidence for Perrett and colleagues' [5] view—initially suggested for nonhuman primates—that gaze processing reflects another person's direction of attention. Note, however, that according to our hypothesis, it is not the gaze-sensitive cells in the STS themselves that represent this mental state, but the interaction between the gaze-processing and the mentalizing system. Together with a recent study in action perception [30], this sophisticated interplay between social perception and social mentalistic beliefs might point toward a more general effect of high-level mental-state attribution in facilitating and shaping the way in which social signals are processed on a lower level.

Experimental Procedures

Observers
Twenty observers (9 female, 11 male, mean 25 years) and 16 observers (13 female, 3 male, mean 25 years) participated in experiment 1 and experiment 2, respectively. In each experiment, one additional observer was excluded because their gaze-direction judgment during the training session was less than 60% correct (more than two standard deviations below the group mean), indicating general problems in judging gaze direction. All but three observers in experiment 1 and two in experiment 2 reported that they were convinced that the prerecorded videos showed two real people. Observers gave written consent, received payment, and were fully debriefed. The study was approved by a local ethics committee. Materials, stimuli, and design are summarized in Figure 1 and described in detail in the Supplemental Experimental Procedures available online.

Analysis
In order to assess the observer's acuity in judging gaze direction, left responses were assigned a 1, straight responses a 0, and right responses a −1. These scores were added up for each test stimulus category (5° left, straight, 5° right) within each test phase, resulting in one combined measure of gaze-direction judgment. The stronger an observer's tendency to judge gaze direction as left, the more positive this combined measure was; a stronger tendency to judge gaze direction as right resulted in a more negative score. Accordingly, a score of 10 indicates that observers always judged gaze direction as left, and a score of −10 indicates that they always judged gaze direction as right. This type of coding is sensitive to the direction of deviation from a correct response and is thus more appropriate than the use of the percentage of straight responses as in previous studies.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01248-2.

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