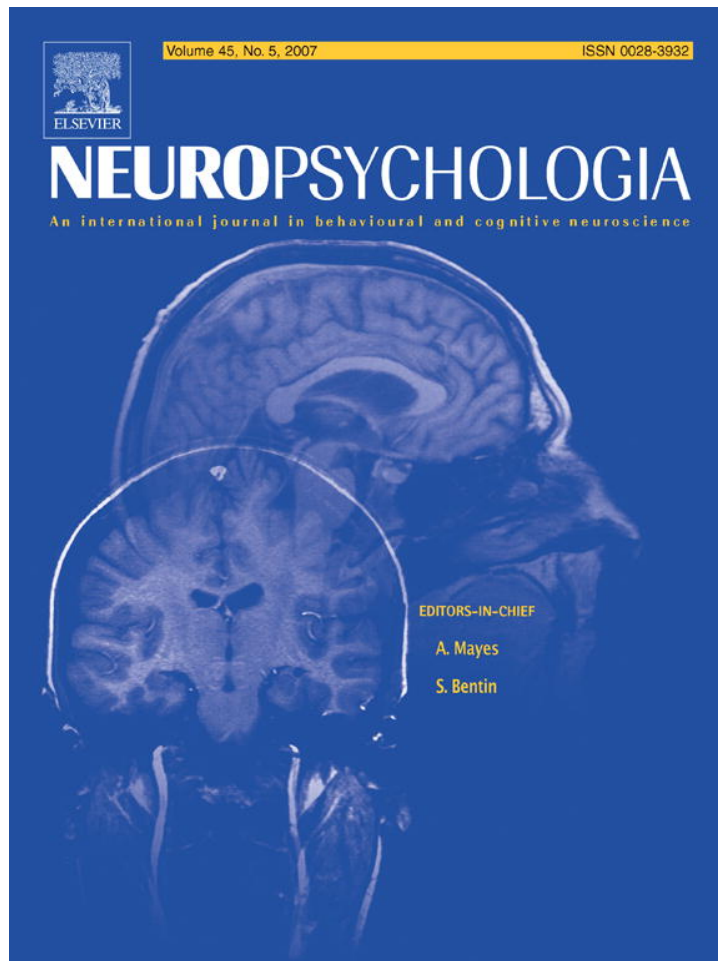


Provided for non-commercial research and educational use only.
Not for reproduction or distribution or commercial use.



This article was originally published in a journal published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues that you know, and providing a copy to your institution's administrator.

All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

Eyes always attract attention but gaze orienting is task-dependent: Evidence from eye movement monitoring

Roxane J. Itier*, Christina Villate, Jennifer D. Ryan

The Rotman Research Institute, Baycrest, Toronto, Canada

Received 26 May 2006; received in revised form 4 September 2006; accepted 10 September 2006
Available online 24 October 2006

Abstract

Eyes and gaze are central to social cognition but whether they attract attention differently depending on the task is unknown. Here, the shift in attention towards the eye region and gaze direction of a perceived face was studied in two tasks by monitoring eye movements. The same face stimuli in front- or 3/4-view, with direct or averted gaze, were used in both tasks. In the *Gaze task*, subjects performed an explicit gaze direction judgment (gaze straight or averted) while in the *Head task* they performed a head orientation judgment (front- or 3/4-view). Gaze processing was evident in both tasks as shown by longer RTs and lower accuracy when head and gaze directions did not match. In both tasks the eye region was the most attended area but the amount of viewing was task-dependent. Most importantly, ~90% of the initial saccades landed in the eye region in the *Gaze task* but only ~50% of them did so in the *Head task*. These saccades were made in the direction signaled by gaze in the *Gaze task* but in the direction signaled by head orientation in the *Head task*. Altogether, these task-modulated behaviors argue against a purely exogenous and automatic orienting-to-gaze mechanism. Based on patient work and neuroimaging studies of gaze processing, we suggest that this task-dependent orienting behavior is rather endogenous and subtended by cortical areas amongst which frontal regions play a central role. We discuss the implications of this finding for clinical populations.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Eyes; Faces; Gaze orienting; Social attention; Social cognition

1. Introduction

The human face is undoubtedly the most important social stimulus our species process everyday and its core feature, the eyes, bear a fundamental role in social cognition. Numerous behavioral and eye movement studies on various face tasks have shown that the eyes are the facial features that are most attended (Althoff & Cohen, 1999; Firestone, Turk-Browne, & Ryan, 2006; Henderson, Williams, & Falk, 2005; Janik, Wellens, Goldberg, & Dell'osso, 1978; Laughery, Alexander, & Lane, 1971; Luria & Strauss, 1978; Schyns, Bonnar, & Gosselin, 2002; Tanaka & Farah, 1993; Vinette, Gosselin, & Schyns, 2004; Walker-Smith, Gale, & Findlay, 1977; Yarbus, 1967). In addition to their role in identity recognition (Ellis, Shepherd, &

Davies, 1979; McKelvie, 1976), the eyes are central to social communication as they indicate emotions, direction of attention and intentions (Baron-Cohen, 1995; Baron-Cohen, Jolliffe, Mortimore, & Robertson, 1997).

The direction of others' attention is mainly indicated by the orientation of the head and by the direction of gaze (Emery, 2000; Langton, 2000; Langton, Watt, & Bruce, 2000). Gaze direction can indicate at what and where someone is looking and possibly why. Our ability to make inferences, to attribute thoughts and intentions to others, is referred to as theory of mind (ToM) (Premack & Woodruff, 1978) and the interpretation of another person's gaze seems to be one of its basic attributes (Baron-Cohen, 1995).

An important yet unresolved question is whether gaze processing is a reflexive or a learned mechanism. One piece of evidence supporting the reflexive view of gaze processing is gaze-orienting behavior. It has been shown that when an irrelevant distractor face is presented centrally at fixation, responses to a peripheral target are faster when the gaze of the face is directed towards the target location compared to when it is directed

* Corresponding author at: The Rotman Research Institute, Baycrest Centre for Geriatric Care, 3560 Bathurst Street, Toronto, Ontario M6A 2E1, Canada. Tel.: +1 416 785 2500x3812; fax: +1 416 785 2862.

E-mail address: ritier@rotman-baycrest.on.ca (R.J. Itier).

towards the location opposite that of the target (Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999; Langton & Bruce, 1999; Vuilleumier, 2002). This orienting mechanism is not simply due to target appearance as it is observed even when a distractor stimulus is presented in the direction opposite to that of the gaze (Friesen, Moore, & Kingstone, 2005). The effect is robust as it has even been observed for simple cartoons with schematic eyes (Friesen & Kingstone, 1998). As it is fast (occurring within a few hundreds of milliseconds), present in infants as early as 3 months of age (Hood, Willen, & Driver, 1998), and observed even though the gaze is irrelevant to the task, does not predict, or is even counter-predictive of target location, this effect has been interpreted as reflecting an automatic, reflexive and stimulus-driven (exogenous) orienting mechanism that cannot be suppressed (Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999; Langton & Bruce, 1999; Mansfield, Farroni, & Johnson, 2003; Ricciardelli, Bricolo, Aglioti, & Chelazzi, 2002). From a survival perspective, such a reflexive mechanism enabling the fast detection of a potential oncoming danger would be extremely useful.

Recently however, the case study of a frontal-lobe patient who could not orient to gaze cues but who could normally orient to unpredictable peripheral cues (Vecera & Rizzo, 2006) challenged the reflexive view of orienting to gaze behavior. Because the reflexive orienting to target was preserved in this patient while gaze orienting was impaired, Vecera and Rizzo (2006) concluded that gaze orienting was an endogenous rather than exogenous mechanism. That is, such orienting occurred in response to internal factors like goals or intentions rather than in response to external factors in the environment. Through development, we would learn to orient attention to the direction of gaze because of its social importance. At the adult stage, the association would be so well learned that it would seem automatic. This “over-learned” association mechanism would depend on cortical rather than subcortical areas, amongst which the medial frontal lobe would play a central role (Vecera & Rizzo, 2006).

The implication of frontal areas in gaze-orienting behavior is consistent with the current literature on gaze processing. Cell recordings have shown face-selective and eye-selective cells in the superior temporal sulcus (STS) of the monkey brain which are sensitive to gaze direction and seem to be part of a larger network specialized in social interactions (Hasselmo, Rolls, & Baylis, 1989; Perrett et al., 1985). Likewise, neuroimaging studies in humans have shown that gaze processing recruits mainly the superior and middle temporal gyus regions (Allison, Puce, & McCarthy, 2000; Hoffman & Haxby, 2000; Hooker et al., 2003; Pelphrey, Singerman, Allison, & McCarthy, 2003; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety, 1998; Wicker, Perrett, Baron-Cohen, & Decety, 2003). Importantly, frontal regions such as medial orbital and prefrontal cortices that are generally recruited in ToM tasks (Adolphs, 1999; Amodio & Frith, 2006; Baron-Cohen et al., 1999; Frith & Frith, 1999) have also been found in simple gaze studies (Calder et al., 2002; Happe et al., 1996; Wicker et al., 1998). Cortical regions involved in gaze processing thus seem part of a larger network involved in theory of mind and social cognition processes.

However, although the frontal case study of Vecera and Rizzo demonstrated the necessary implication of frontal areas in gaze-orienting behavior, it did not prove the non-reflexive nature of this mechanism. Orienting to gaze could rely on different or additional brain structures than orienting to peripheral cues, but it could still be reflexive and dependent on frontal areas. Showing an absence of reflexive orienting to gaze cues in normal controls would be a clearer demonstration of the non-automaticity of this behavior. This possibility is explored in the present study.

The reflexive nature of the gaze-orienting behavior was investigated in normal subjects on two different tasks using the same front- and three-quarter-view face stimuli. It was hypothesized that a truly automatic and reflexive mechanism should occur regardless of the task demands, paradigm or stimuli used. Subjects performed an explicit gaze direction judgment (Gaze task) in which they discriminated between straight and averted gazes, and a head orientation judgment (Head task) in which they discriminated between front-view and three-quarter-view faces. Attention to the eyes/gaze was not required to perform this latter task. In addition to classic accuracy and reaction time measures, eye movements were recorded. Eye movement measures such as fixation location and duration of viewing time provide indications of what part of the face a subject attended at any given time, and for how long (Firestone et al., 2006; Henderson et al., 2005; Yarbus, 1967). In addition, analyses of the direction of saccadic eye movements provide information on where the subject is moving his/her eyes immediately following stimulus onset.

It was predicted that if gaze orienting were a reflexive mechanism, the eyes should be the most attended feature as measured by viewing time and fixation location, in both tasks. Furthermore, the very first saccade initiated after stimulus onset should also go directly to the eye region and should be made in the direction signaled by gaze, regardless of the task. In contrast, differential eye movement patterns between the two tasks would argue against a pure reflexive gaze-orienting mechanism and would suggest that attention to the eyes and/or gaze is goal-oriented and modulated by task demands. In other words, if gaze orienting is reflexive, making a judgment about head orientation, which does not require processing of the eyes and/or gaze, should trigger similar gaze-orienting behavior and eye movements as making an explicit judgment about the gaze direction.

2. Method

2.1. Participants

Fifteen young and healthy volunteers from the Toronto area (21–35 years) were tested and paid for their participation. One subject was rejected due to a computer error in data acquisition. They all had normal or corrected-to-normal vision. All signed a written informed consent that was approved by the Ethics Research Board of Baycrest.

2.2. Stimuli

Stimuli consisted of grayscale photographs of twelve unique faces (half female) taken from a previous study (George, Driver, & Dolan, 2001), with neutral expression. Each face was photographed in a front-view and with the face turned 30° to the right (3/4-view), with the eyes looking straight ahead at the

camera or 30° to the right, yielding four main conditions: head-turned-gaze-averted, head-turned-gaze-straight, head-front-gaze-averted, head-front-gaze-straight. These four original pictures were then mirror-reversed using Photoshop, to avoid any bias between the right and left sides, generating eight conditions in total according to a full factorial design of head orientation (3/4-view or front-view) × gaze direction (straight or averted) × side (left or right). For all analyses, left and right sides were collapsed except when explicitly mentioned. Scrambled faces of the front-view-gaze-straight pictures were generated using a home-made Matlab program and were used as fillers.

2.3. Design and procedure

Participants were comfortably seated in an adjustable chair in front of a 19-inch Dell M991 monitor (resolution 1024 × 768) situated 60 cm in front of them. Stimuli were presented centrally on the screen (6.5° × 8.5° visual angle) for 500 ms with a random ISI between 2000 and 2500 ms during which a centered fixation cross appeared. Subjects performed two different tasks. In the Gaze task, subjects discriminated between straight and averted gaze regardless of head orientation (Is the person looking at you or away?). In the Head task, they discriminated between front- and 3/4-view faces regardless of gaze direction. In the latter task, subjects were explicitly told that they did not need to look at the eyes as gaze direction was totally irrelevant. Subjects responded with both hands, using a left and a right buttons situated on a keypad that they were holding. In both tasks, subjects were required to refrain from responding to scrambled stimuli.

Four blocks of 108 stimuli each were presented, alternating between the two tasks (two blocks per task). Block and button orders were counterbalanced across subjects and tasks. A nine trial practice block was given before the initial head and gaze judgment blocks. In each block, each individual face was presented in each of the 8 conditions and repeated twice, along with 12 scrambled stimuli (fillers). Thus, in each task there were 48 trials for each of the 8 conditions (12 faces × 2 presentations × 2 blocks), for a total of 96 trials for each of the four main conditions when left and right sides were collapsed. Faces were semi-randomized with the constraint that the face of the same individual in a particular head orientation and gaze direction would never be followed or preceded by the same face with a different gaze direction (e.g. head-averted-gaze-straight would never follow or precede head-averted-gaze-averted for the same individual face). This was to prevent the perception of gaze motion. Breaks were given between blocks. Subjects were told to perform the tasks as quickly and accurately as possible. Responses and reaction times were recorded.

Eye movements were monitored using an SR Research Ltd., EyeLink II system (video-based eye movement monitoring device), consisting of a lightweight head-and-mounted eye-tracking system allowing subject head motion and speech. Two custom-built ultra-miniature high-speed cameras took simultaneously 250 images/s (250 Hz sampling rate) of both eyes positions to provide binocular eye tracking. Subjects were explicitly told not to move their eyes during the stimulus presentation and to fixate on the centered fixation cross between trials. Eye movements were calibrated before each block using a nine-point calibration accuracy test. Calibration was repeated if the error at any point was more than 1°, or if the average error for all points was greater than 0.5°. Subjects initiated each trial by fixating on the central fixation cross and pressing a button on the keypad.

Saccades were defined as a movement of more than 0.5° of visual angle that had an acceleration and a velocity of at least 3800°/s² and 22°/s, respectively, so saccades could be detected with a high sensitivity. Saccade offset (fixation onset) was defined as four continuous samples in which the velocity and acceleration were below the above noted values.

2.4. Data analysis

Accuracy rates, reaction times and eye movement patterns were examined and compared among face conditions and between tasks. The eye movements recorded to the scrambled stimuli were not analyzed. As the stimuli were on the screen for a short time and subjects were not supposed to move their eyes, few eye movements resulted. Predictions regarding viewing time, fixations, number of saccades and their direction involved mainly the eye region so each stimulus was divided into two areas of interest (AOI)—the “eye” region including the

eyebrows and the area between the eyes, and the “lower face” region, comprising the rest of the face under the eye region. The upper face area, i.e. the rest of the face situated above the eye area, was not analyzed due to too few eye movements in that region. As feature visibility and visual extent varied across conditions (due to head orientation), and because few eye movements in general were recorded, the AOIs were not further subdivided.

The proportion of viewing time directed to each AOI as a function of the total time spent on the whole face area, and the proportion of fixations directed to each AOI as a function of the total number of fixations on the whole face, were analyzed. Furthermore, for each subject, each condition and each task, the total number of first saccades following stimulus onset and landing in each AOI, as well as the direction of the first saccade landing in the eye region, were analyzed. The leftward or rightward saccade directions were defined according to whether the end position of the eyes was to the left or to the right of their initial position at fixation.

Responses obtained to left- and right-sided stimuli were combined for all measures except for the direction of the first saccades (i.e. for head front, left- and right-averted gaze were combined to yield the head-front-gaze-averted condition, etc.). Within-subject factors for the ANOVA tests were task (Gaze or Head task), head orientation (front-view or 3/4-view), gaze direction (averted or straight/direct) and AOI (eye or lower face area). Paired-sample *t*-tests were also used to compare conditions.

3. Results

3.1. Behavioral data

Accuracy and RT measures were analyzed using a 2 (task) × 2 (head orientation) × 2 (gaze direction) ANOVA.

3.1.1. Hit rates

Subjects were more accurate in the Head than in the Gaze task (main effect of task, $F(1, 13) = 18.5, p < .001$). The task × head orientation ($F(1, 13) = 8.19, p < .05$), task × gaze direction ($F(1, 13) = 5.63, p < .05$), and task × head × gaze ($F(1, 13) = 20.99, p < .0001$) interactions were significant. They were due to a task difference mainly on the incongruent conditions (i.e. when head and gaze direction did not match) while the congruent conditions (head-turned-gaze-averted and head-front-gaze-straight) yielded similar accuracy rates between tasks (Fig. 1A). The ANOVAs were re-run separately for each task.

In the Gaze task, the main effects of head orientation ($F(1, 13) = 38.36, p < .0001$) and gaze direction ($F(1, 13) = 6.67, p < .05$) were due to lower accuracy for 3/4-view heads and for straight gaze, respectively. The head orientation by gaze direction interaction ($F(1, 13) = 47.77, p < .0001$) was due to higher accuracy for straight than averted gaze in front-view faces ($t(13) = -5.71, p < .0001$) while accuracy was higher for averted than straight gaze for 3/4-view faces ($t(13) = 6.03, p < .0001$) (Fig. 1A). This reflected higher rates for congruent conditions.

In the Head task, the head orientation by gaze direction interaction was also significant ($F(1, 13) = 7.26, p < .02$) but no main effects were found. Post hoc *t*-tests revealed no significant difference between gaze directions for 3/4-view heads ($p = .14$) but better accuracy for straight than averted gaze for front-view faces ($t(13) = -2.7, p < .02$) (Fig. 1A).

3.1.2. Reaction times

Subjects were faster in the Head than in the Gaze task (main effect of task, $F(1, 13) = 10.29, p < .01$). The task by head ori-

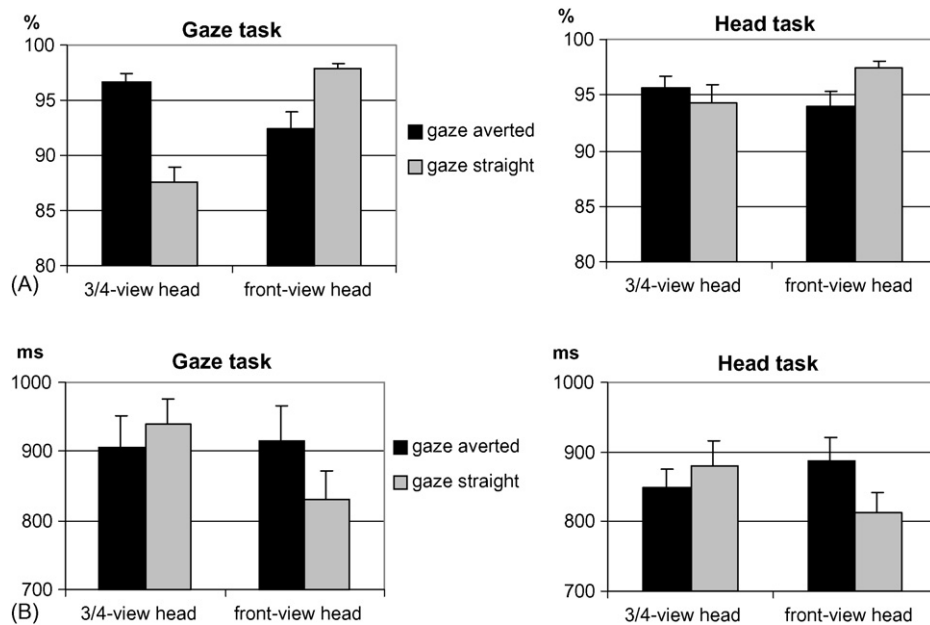


Fig. 1. (A) Accuracy and (B) mean reaction times obtained as a function of head orientation and gaze direction (vertical bars = standard errors).

entation interaction ($F(1, 13) = 5.86, p < .05$) was due to similar RTs in the two tasks for the head-front-gaze-straight condition while RTs were longer in the other conditions for the Gaze task (Fig. 1B). This suggests the RT differences were not due to speed-accuracy trade-off.

In the Gaze task, the main effects of head orientation ($F(1, 13) = 22.19, p < .0001$) and gaze direction ($F(1, 13) = 6.39, p < .025$) were significant. Most importantly, the significant head orientation by gaze direction interaction ($F(1, 13) = 33.28, p < .0001$) was due to longer reaction times for straight than averted gaze in 3/4-view faces ($t(13) = -2.52, p < .03$) while RTs were longer for averted than straight gaze in front-view faces ($t(13) = 5.48, p < .0001$). This thus reflected longer RTs for incongruent conditions (Fig. 1B). The fastest RTs were found for the head-front-gaze-straight condition.

In the Head task, the effect of gaze direction was significant ($F(1, 13) = 14.86, p < .005$). Again, the head orientation by gaze direction interaction ($F(1, 13) = 22.1, p < .0001$) was due to longer RTs for incongruent conditions (Fig. 1B). Longer reaction times were found for straight than averted gaze in 3/4-view faces ($t(13) = -3.23, p < .007$) while RTs were longer for averted than straight gaze in front-view faces ($t(13) = 5.02, p < .0001$). In summary, the head-front-gaze-straight condition yielded the best accuracy and the fastest reaction times in both tasks. Incongruent conditions increased RTs and decreased accuracy, but the effect was more pronounced in the Gaze than in the Head task, especially for the head-turned-gaze-straight condition.

3.2. Eye movement data

The importance of the eye region was assessed with viewing time and fixation measures.

3.2.1. Proportion of viewing time

The average proportion of viewing time was analyzed using a 2 (task) \times 2 (head orientation) \times 2 (gaze direction) \times 2 (AOI) ANOVA.

The proportion of total viewing time was higher in the eye than in the lower face area for both tasks (AOI effect, $F(1, 13) = 138.66, p < .0001$) (Fig. 2). However, a task by AOI interaction ($F(1, 13) = 9.45, p < .009$) reflected a greater proportion of viewing time in the eye region for the Gaze than the Head task while the opposite was found for the lower face area (Fig. 2). Post hoc ANOVAs confirmed this task effect for the eye region ($F(1, 13) = 9.43, p < .009$) and the lower face area ($F(1, 13) = 9.46, p < .009$) analyzed separately. The AOI by head orientation interaction ($F(1, 13) = 16.83, p < .001$) was due to a greater proportion of viewing time in the lower face region for 3/4-view faces compared to front-view faces ($p < .001$), whereas in the eye region a greater proportion of viewing time was found for front-view than 3/4-view faces ($p < .002$) (Table 1).

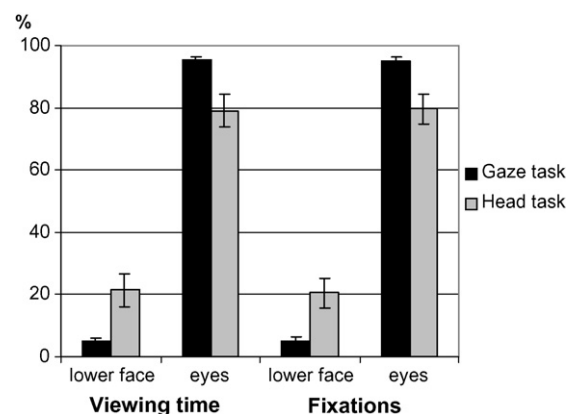


Fig. 2. Proportion of total viewing time and fixations directed to the eye and the lower face regions for both tasks (vertical bars = standard errors).

Table 1

Proportion of total viewing time and fixations as a function of head orientation and area of interest (both tasks combined)

	Lower face area		Eye area	
	3/4-view heads	Front-view heads	3/4-view heads	Front-view heads
Viewing time (%)	14.3 (3.4)	11.9 (3)	86.2 (3.3)	88.5 (2.9)
Fixations (%)	13.7 (3.3)	11.4 (2.8)	86.5 (3.1)	88.7 (2.7)

In the lower face area, a greater proportion of viewing time and fixations were found for faces seen in 3/4-views, while in the eye region a greater proportion of viewing time and fixations were found for front-view faces (standard errors in parenthesis).

3.2.2. Proportion of fixations

As done for the proportion of viewing time, the average proportion of total fixations was analyzed using a 2 (task) \times 2 (head orientation) \times 2 (gaze direction) \times 2 (AOI) ANOVA. Very similar results as for the proportion of viewing time were found.

For both tasks more fixations were directed to the eye than to the lower face area (effect of AOI, $F(1, 13) = 161.56$, $p < .0001$). The task by AOI interaction was significant ($F(1, 13) = 10.97$, $p < .006$) and t -tests revealed that a greater proportion of fixations was directed to the eye region in the Gaze compared to the Head task ($p < .005$), while the opposite was found for the lower face region ($p < .006$) (Fig. 2). Again, the AOI by head orientation interaction ($F(1, 13) = 11.62$, $p < .005$) was due to a greater proportion of fixations directed to the lower face region for 3/4-view than front-view faces ($p < .004$) while more fixations were directed to the eye region for front-view compared to 3/4-view faces ($p < .006$) (Table 1).

In summary, greater proportions of viewing time and fixations were directed to the eye region than to the lower face area, reflecting the importance of the eye region in both tasks. However, increased sampling of the eye region occurred for the Gaze than the Head task while the opposite was found for the lower face area. These results suggest a task modulation in the importance of the eye region and goal-oriented eye movements in service of the task at hand.

Evidence of increased viewing time and fixations reveals the importance of the eye region but does not reveal whether there is orienting to gaze. To assess this, the first saccade made after stimulus onset was analyzed. To the extent that orienting is automatic, one would predict that the very first saccades made by subjects after stimulus onset should go directly to the eye region regardless of task instructions, and that the direction of these saccades landing in the eye region should follow the gaze direction. The analysis thus focused on (1) the total number of initial saccades after stimulus onset directed to the eye versus the lower face regions and (2) the direction of those saccades that landed in the eye region.

3.2.3. First saccades made after stimulus onset

The trials in which saccades were made were analyzed and the focus was on the initial saccade. The total number of these initial saccades made after stimulus onset (see Table 2), was analyzed using a 2 (task) \times 2 (head orientation) \times 2 (gaze direction) \times 2 (AOI) ANOVA.

A significant effect of task ($F(1, 13) = 151.19$, $p < .0001$) was due to more saccades found in the Gaze than in the Head task. More saccades landed in the eye region than in the lower face

Table 2

Total number of initial saccades after stimulus onset, made in the three areas of interest in each task (saccades were summed across all subjects and all conditions)

	Eye area	Lower face area	Upper face area	Total
Gaze task	3551 (90.2%)	369 (9.3%)	18 (0.5%)	3938 (100%)
Head task	1431 (47.7%)	1527 (50.9%)	41 (1.4%)	2999 (100%)

The corresponding percentage of initial saccades landing in each AOI is in parenthesis. Only the eye and the lower face areas were subsequently analyzed (see Figs. 3 and 4).

area (effect of AOI, $F(1, 13) = 45.5$, $p < .0001$). However, the task by AOI interaction ($F(1, 13) = 79.6$, $p < .0001$) was due to more saccades landing in the eye region for the Gaze than the Head task (confirmed by a main effect of task when the eye region was analyzed separately, $F(1, 13) = 113.04$, $p < .0001$), while more saccades were found in the lower face area for the Head than the Gaze task (task effect for the lower area, $F(1, 13) = 9.58$, $p < .009$) (Fig. 3). The eye versus lower face area difference in the Head task was not significant ($p > .5$ for the AOI factor in the Head task).

As seen in Table 2, the first eye movements made by subjects landed mostly in the eye region in the Gaze task (in $\sim 90\%$ of instances, while $\sim 9\%$ landed in the lower face area) but as often in the eye than in the lower face area in the Head task ($\sim 48\%$ and $\sim 51\%$, respectively). In addition, no effects of gaze direction were found. These results are inconsistent with a pure automatic and reflexive gaze-orienting mechanism.

However, it is possible that the influence of gaze direction would be observed if the saccades that landed in the eye region were analyzed separately from those landing in the lower face area. The eye and the lower face areas were thus analyzed separately.

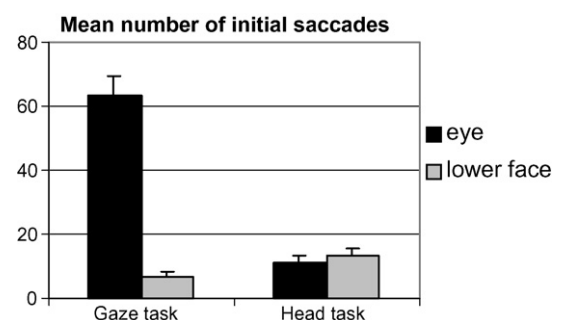


Fig. 3. Mean number of first saccades made to the eye region and to the lower face area as a function of task (vertical bars = standard errors).

Table 3

Total number of initial saccades landing in the eye region and directed to the left or to the right of the fixation cross, for each task and each condition

	Left-oriented stimuli				Right-oriented stimuli			
	Head (3/4-view)- gaze-averted	Head (3/4-view)- gaze-straight	Head-front- gaze-averted	Head-front- gaze-straight	Head (3/4-view)- gaze-averted	Head (3/4-view)- gaze-straight	Head-front- gaze-averted	Head-front- gaze-straight
Gaze task								
Left saccade	200	171	259	255	103	102	170	172
Right saccade	79	105	105	108	187	145	183	166
Head task								
Left saccade	140	134	94	81	60	54	80	88
Right saccade	17	23	55	43	136	134	61	49

Saccades were summed across all subjects.

In the lower face area, no main effects of Head or Gaze and no interactions were found. In the eye region, no main effects of Head or Gaze were found. However, the task \times gaze interaction ($F(1, 13) = 14.7, p < .002$) was due to more saccades landing in the eye region for averted than straight gaze in the Gaze task ($p < .02$) while the opposite was found in the Head task ($p < .02$) (Fig. 4). A trend was found for the head \times gaze interaction ($p < .07$). The three-way interaction of task \times head \times gaze was also significant ($F(1, 13) = 7.83, p < .02$). This effect was due to more saccades landing in the eye region for straight than averted gaze for 3/4-view faces ($t(13) = -2.93, p < .02$) in the Head task only. In the Gaze task, there was no interaction of head orientation and gaze direction.

Thus, an influence of gaze direction was found when the saccades that landed in the eye region were analyzed separately. However, this influence was different depending on the task, thus not supporting an automatic and reflexive gaze-orienting mechanism.

It still remains possible that when the eye region is fixated, orienting to the gaze direction nonetheless occurs in a reflexive manner. Finding that the saccades landing in the eye region follow the direction of the gaze stimulus regardless of task demands would provide some evidence for a reflexive gaze-orienting behavior. The direction of these saccades landing in the eye region was thus analyzed.

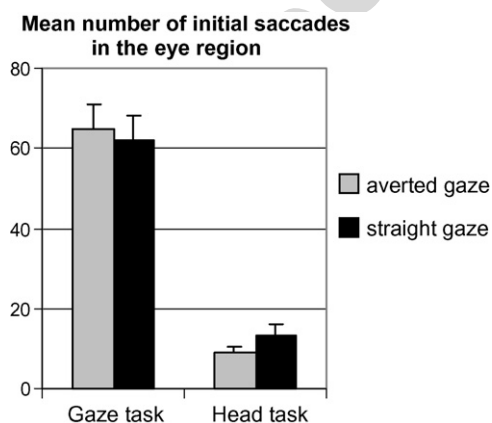


Fig. 4. Mean number of first saccades made to the eye region as a function of gaze direction and task (vertical bars = standard errors).

3.2.4. Direction of first saccades landing in the eye region

If the orienting to gaze behavior is present, and reflected in the first saccades landing in the eye region, more leftward saccades should be found when the gaze is averted to the left compared to when gaze is straight and more rightward saccades should be found when the gaze is averted to the right compared to when it is straight. Since the number of saccades that landed in the eye region was different in the two tasks (Table 3), the saccade direction was analyzed in each task separately. A 2 (head orientation) \times 2 (gaze direction) ANOVA was run on the number of leftward saccades for the left-sided stimuli and on the number of rightward saccades for the right-sided stimuli.

In the Gaze task, an effect of gaze was found for the rightward saccades ($F(1, 13) = 10.35, p < .007$), and a trend was found for leftward saccades ($F(1, 13) = 3.5, p < .09$). This was due to more leftward saccades for left-averted gaze than straight gaze stimuli and more rightward saccades for right-averted than straight gaze stimuli (Fig. 5A). No effects of head orientation or head by gaze interaction were found (Fig. 5B). Thus, in the Gaze task, saccades were made in the direction of perceived gaze.

In the Head task, no effect of gaze was found for the leftward or rightward saccades (Fig. 5A). However, an effect of head orientation was found for the rightward saccades ($F(1, 13) = 8.16, p < .02$) due to more rightward saccades when the head was turned to the right compared to when it was in front-view (Fig. 5B). For the leftward saccades, no significant effect of head orientation was found although a trend for more leftward saccades when the head was turned to the left can be seen in Fig. 5B. Thus, in the Head task, saccades were not made in the direction of gaze, but mainly in the direction signaled by head orientation.

4. Discussion

The reflexive nature of the orienting to gaze behavior was investigated in two tasks that required an explicit gaze direction judgment (Gaze task) or a head orientation judgment (Head task), by measuring behavioral responses as well as eye movement patterns. The behavioral data reproduced previous findings and the eye movement results showed that (1) the eye region was the most attended feature in both tasks, even in the Head task where gaze was irrelevant and (2) the gaze-orienting behavior

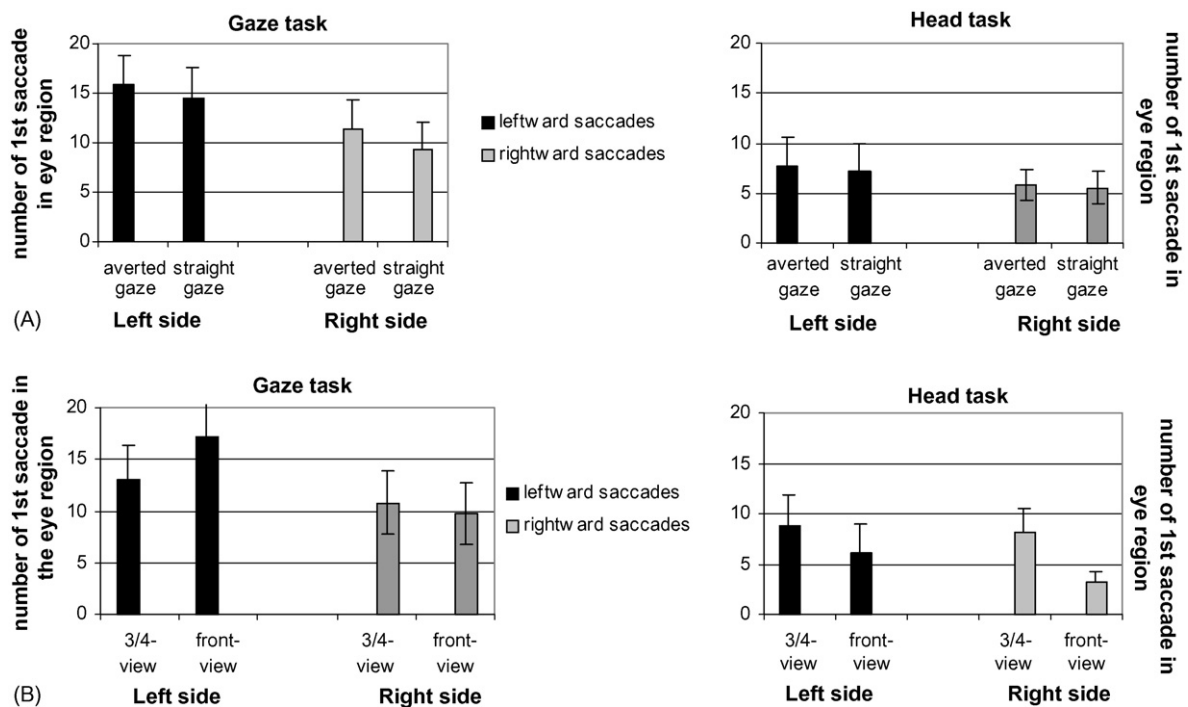


Fig. 5. Mean number of first saccades made in the eye region for both tasks (A) as a function of gaze direction and (B) as a function of head orientation (vertical bars = standard errors).

was modulated by task demands, suggesting it is not automatic and reflexive. We discuss these main results in turn.

In both tasks, behavioral performances showed the influence of gaze on cognitive processing as slower reaction times and lower performances were found for incongruent stimuli, when head orientation and gaze direction did not match, consistent with previous work (Vuilleumier, George, Lister, Armony, & Driver, 2005). Slower RTs have been reported for faces with straight/direct gaze (Senju & Hasegawa, 2005; Vuilleumier et al., 2005), and were thought to reflect an enhanced and thus longer processing of faces with direct gaze (Vuilleumier et al., 2005), or a slower attentional disengagement from the face because of its direct gaze (Senju & Hasegawa, 2005). However, faster RTs for direct gaze have also been reported (Macrae, Hood, Milne, Rowe, & Mason, 2002). In the present study, both faster and slower RTs were found for direct gaze, depending on the head orientation, the fastest condition being the front-view face with direct gaze for both tasks. These findings reconcile discrepant results reported in the literature and show that our tasks were appropriately measuring gaze processing effects. Taken in isolation, these behavioral data suggest that gaze was processed even in the Head task where it was irrelevant and thus they could be taken as reflecting automatic and reflexive gaze processing, as suggested by the widely documented orienting to gaze behavior literature (Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999; Langton & Bruce, 1999; Mansfield et al., 2003; Ricciardelli et al., 2002; Vuilleumier, 2002). However, accuracy and RT measures can only comment on the outcome of processing, rather than revealing the nature of processing itself. The eye movement data add an important piece of information regarding what subjects attend *first* and,

in fact, show that orienting to gaze direction is not a reflexive mechanism.

In the present study, we reasoned that if attraction to the eyes were really a reflexive mechanism, subjects should orient their eye movements to the eye region of the face immediately, that is, the initial saccade following stimulus onset should go to the eye region and should be made in the direction signaled by gaze. In contrast, we found that most first saccades made after stimulus onset landed in the eye region in the Gaze task (~90%) but as many saccades landed in the eyes as in the lower face area in the Head task (~50%). The saccades that landed in the eye region were made in the direction of the gaze in the Gaze task but mainly in the direction of the head in the Head task. Thus, gaze orienting was found only when an explicit gaze direction judgment was required but not when gaze was irrelevant to the task as in the Head task. Furthermore, although gaze direction influenced the saccades that landed in the eye region, this influence was different depending on the task as suggested by more saccades for averted gaze in the Gaze task but more saccades for straight gaze in the Head task. Altogether, these results argue against an automatic and reflexive gaze-orienting mechanism.

Two previous studies reported cue-driven saccades made spontaneously in the direction of gaze rather than in the direction of the target (Mansfield et al., 2003; Ricciardelli et al., 2002). However, these studies, as well as all previously reported gaze-orienting studies, used a cueing paradigm (Driver et al., 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999; Mansfield et al., 2003; Ricciardelli et al., 2002) and this may be the reason for these apparently reflexive effects. By appearing suddenly on the screen in cueing paradigms, faces with averted eyes may in fact trigger movement orienting rather than gaze orienting

(Vecera & Rizzo, 2006). When tasks are used where the gaze does not cue a target location, the orienting to gaze is found only when subjects are explicitly required to attend the gaze. The widespread use of front-view faces may also be the reason for finding gaze-orienting effects as when faces were in 3/4-view, one study failed to find such an effect (Hietanen, 1999).

In contrast to the reflexive view, our results suggest goal-oriented eye movements in service of the task at hand. While the eyes were necessary to perform the Gaze task, it seems plausible that the lower face area was the most useful feature to perform the Head task as it contains the chin and the cheeks which are very distinct in a 3/4-view compared to a front-view face. The results of increased sampling of the eye region in the Gaze task but increased sampling of the lower face area for the Head task also support a task-dependent attraction to the eyes and lower face area, further arguing against automaticity. These task-oriented eye movements support the diagnostic information theory (Schyns et al., 2002) that certain facial features are preferentially used for certain tasks (e.g. the eyes in gender categorization, the mouth in expression categorization (Schyns et al., 2002; Vinette et al., 2004)).

Although we found that orienting to gaze is not reflexive, longer viewing time and more fixations were directed to the eye region compared to the rest of the face, in both tasks. This reflects the prevalence of the eye region as reported by numerous previous studies (Althoff & Cohen, 1999; Firestone et al., 2006; Henderson et al., 2005; Janik et al., 1978; Laughery et al., 1971; Luria & Strauss, 1978; McKelvie, 1976; Tanaka & Farah, 1993; Vinette et al., 2004; Walker-Smith et al., 1977; Yarbus, 1967). This attraction to the eyes, which is present in infancy (Maurer, 1985), could be due to the social aspect of eyes, mainly reflected by direct gaze. The RT data support the idea that direct gaze is special and influences the speed of face processing (Hood, Macrae, Cole-Davies, & Dias, 2003; Macrae et al., 2002; Vuilleumier et al., 2005) but that this depends on head orientation, in agreement with the idea that head orientation modulates gaze perception (Emery, 2000; Hietanen, 1999; Langton, 2000; Langton et al., 2000).

In real life situations, a front-view face looking straight at you signals the possibility of a social interaction, while the same front-view face with averted gaze signals the person is looking at something other than you. The eye-to-eye gaze is also a threat signal in most primate species (Emery, 2000) and many studies suggest a specific role of direct gaze, supported by investigations in clinical populations and neuroimaging data.

Faces with direct gaze are encoded and recognized better than faces with deviated gaze for both adults and 6–7-year-old children (Hood et al., 2003; Vuilleumier et al., 2005) and similar findings have been reported for 4-month-old infants (Farroni, Massaccesi, Menon, & Johnson, 2006). Infants (Hains & Muir, 1996) and even neonates (Farroni, Csibra, Simion, & Johnson, 2002), discriminate between averted and direct gaze and prefer direct gaze faces because they engage in social contact (Farroni et al., 2006; Hains & Muir, 1996; Hood et al., 1998; Maurer, 1985). Modulations of the activation of the amygdala, a subcortical structure involved in gaze processing (Young et al., 1995) and in social emotions such as fear (Adolphs, 2003),

have been reported for direct gaze perception (Hooker et al., 2003; Kawashima et al., 1999). Similarly, the fusiform gyrus involved in face processing (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997) seems more active following direct than averted gaze (George et al., 2001; Pageler et al., 2003). Autistic and Asperger syndrome (AS) patients, who are impaired at ToM and cannot infer mental states from the eyes (Baron-Cohen, 1995; Baron-Cohen et al., 1997, 1999), seem to avoid eye contact and fixate less on the eyes than control subjects (Dalton et al., 2005; Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Langdell, 1978; Pelphrey et al., 2002). This gaze avoidance could be the cause of the abnormal activation of the fusiform gyrus reported in some neuroimaging studies of autism (Critchley et al., 2000; Dalton et al., 2005; Ogai et al., 2003; Schultz & Klin, 2002). All these data suggest a strong link between the processing of direct gaze and the longer viewing time of the eye region.

Our results are consistent with the idea that gaze orienting, rather than being reflexive and exogenous, could be learned and endogenous (Vecera & Rizzo, 2006). Based on a frontal patient case who could not orient to gaze or to words but who could normally orient to other peripheral cues, Vecera and Rizzo (2006) hypothesized that orienting to gaze was an over-learned association mechanism dependent on the frontal lobes. This mechanism would be similar for gaze, words or symbols like arrows, but different from the reflexive orienting to peripheral targets subtended by subcortical areas such as the superior colliculus (Klein, 2000; Sereno, Briand, Amador, & Szapiel, 2006). There is converging evidence that subcortical structures such as the amygdala, the superior colliculus and the pulvinar still play a role in face detection in adults (Johnson, 2005) and some, e.g. the amygdala involved in gaze processing (Young et al., 1995), could thus be involved in the gaze-orienting mechanism. However, due to the social importance of eyes and their involvement in social cognition, there could be an increased reliance on cortical structures for gaze orienting with increasing age, as seen for faces (Johnson, 2005). The association mechanism between gaze and its direction could thus be an acquired skill emerging with the maturation of the frontal lobes and other cortical areas, consistent with the neuroimaging literature on gaze processing.

Our results that gaze orienting and attraction to the eye region are task-dependent could have important consequences for clinical populations who present theory of mind deficits. As mentioned previously, the development of gaze processing seems to be a milestone for the later developing ToM processes (Baron-Cohen, 1995) and in adults, processing of gaze recruits some of the frontal areas involved in ToM (Amodio & Frith, 2006; Calder et al., 2002; Frith & Frith, 1999; Happe et al., 1996; Wicker et al., 1998). These frontal areas also seem necessary for the normal gaze-orienting behavior (Vecera & Rizzo, 2006) which is driven by the perceived social relevance of gaze (Ristic et al., 2005). Moreover, as shown in the present study, the general attraction to the eye region is increased when explicit processing of gaze is required. Thus, by voluntarily focusing their attention onto the eye gaze of faces, patients impaired at ToM could overcome part of their deficits or at least decrease their social impairments. This possibility is supported by the case of a patient who was unable

to extract emotional information from the eyes after bilateral amygdala damage (Adolphs et al., 2005), a deficit linked to a lack of spontaneous fixations on the eye region. When explicitly told to look at the eyes, her recognition of fearful faces became entirely normal (Adolphs et al., 2005). Possible rehabilitation procedures focusing on the eyes and the direction of gaze could thus be applied to autistic spectrum disorder patients and to medial frontal-lobe patients also impaired at ToM (Mah, Arnold, & Grafman, 2004; Stuss, Gallup, & Alexander, 2001). Further work needs to determine whether such rehabilitation procedures can decrease social impairments in these populations.

5. Conclusion

The present study confirmed the importance of the eye region in face processing, the modulation of gaze perception by head orientation and the special role played by direct gaze. It extends previous studies by showing that the eye region attracts overt attention even when it is irrelevant to perform the task, but that such attraction can be modulated by task demands. The results also showed that gaze orienting can be found in tasks other than cueing paradigms, but that it is nevertheless task-dependent, arguing against a pure reflexive and exogenous mechanism. Two different processes seem to occur when viewing a face: a gaze-orienting mechanism and an overt attraction of attention by the eye region. Both are likely endogenous rather than reflexive mechanisms. Their development seems to be due to the social relevance of gaze, a learnt skill presumably subtended by the development of the frontal lobes.

Acknowledgements

We thank Dr. Nathalie George for lending us part of her stimuli. This work was supported by funding from CIHR, NSERC and the Heart and Stroke Foundation Centre for Stroke Recovery.

References

- Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Sciences*, 3(12), 469–479.
- Adolphs, R. (2003). Is the human amygdala specialized for processing social information? *Annals of the New York Academy of Sciences*, 985, 326–340.
- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, 433(7021), 68–72.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267–278.
- Althoff, R. R., & Cohen, N. J. (1999). Eye-movement-based memory effect: A reprocessing effect in face perception. *Journal of Experimental Psychology: Learning Memory and Cognition*, 25(4), 997–1010.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, 7(4), 268–277.
- Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind*. Cambridge: MIT Press.
- Baron-Cohen, S., Jolliffe, T., Mortimore, C., & Robertson, M. (1997). Another advanced test of theory of mind: Evidence from very high functioning adults with autism or asperger syndrome. *Journal of Child Psychology and Psychiatry*, 38(7), 813–822.
- Baron-Cohen, S., Ring, H. A., Wheelwright, S., Bullmore, E. T., Brammer, M. J., Simmons, A., et al. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience*, 11(6), 1891–1898.
- Calder, A. J., Lawrence, A. D., Keane, J., Scott, S. K., Owen, A. M., Christoffels, I., et al. (2002). Reading the mind from eye gaze. *Neuropsychologia*, 40(8), 1129–1138.
- Critchley, H. D., Daly, E. M., Bullmore, E. T., Williams, S. C., Van Amelsvoort, T., Robertson, D. M., et al. (2000). The functional neuroanatomy of social behaviour: Changes in cerebral blood flow when people with autistic disorder process facial expressions. *Brain*, 123(Pt 11), 2203–2212.
- Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H. H., et al. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature Neuroscience*, 8(4), 519–526.
- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*, 6(5), 509–540.
- Ellis, H. D., Shepherd, J. W., & Davies, G. M. (1979). Identification of familiar and unfamiliar faces from the internal and external features: Some implications for theories of face recognition. *Perception*, 8, 431–439.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24(6), 581–604.
- Farroni, T., Csibra, G., Simion, G., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences of the United States of America*, 99(14), 9602–9605.
- Farroni, T., Massaccesi, S., Menon, E., & Johnson, M. H. (2006). Direct gaze modulates face recognition in young infants. *Cognition*, in press.
- Firestone, A., Turk-Browne, N. B., & Ryan, J. D. (2006). Age-related deficits in face recognition are related to underlying changes in scanning behavior. *Aging, Neuropsychology and Cognition*, in press.
- Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review*, 5(3), 490–495.
- Friesen, C. K., Moore, C., & Kingstone, A. (2005). Does gaze direction really trigger a reflexive shift of spatial attention? *Brain and Cognition*, 57(1), 66–69.
- Frith, C. D., & Frith, U. (1999). Interacting minds—A biological basis. *Science*, 286(5445), 1692–1695.
- George, N., Driver, J., & Dolan, R. J. (2001). Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *Neuroimage*, 13(6 Pt 1), 1102–1112.
- Hains, S. M., & Muir, D. W. (1996). Infant sensitivity to adult eye direction. *Child Development*, 67(5), 1940–1951.
- Happe, F., Ehlers, S., Fletcher, P., Frith, U., Johansson, M., Gillberg, C., et al. (1996). ‘Theory of mind’ in the brain. Evidence from a PET scan study of Asperger syndrome. *Neuroreport*, 8(1), 197–201.
- Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research*, 32, 203–218.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223–233.
- Henderson, J. M., Williams, C. C., & Falk, R. J. (2005). Eye movements are functional during face learning. *Memory & Cognition*, 33(1), 98–106.
- Hietanen, J. K. (1999). Does your gaze direction and head orientation shift my visual attention? *Neuroreport*, 10(16), 3443–3447.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3(1), 80–84.
- Hood, B. M., Macrae, C. N., Cole-Davies, V., & Dias, M. (2003). Eye remember you: The effects of gaze direction on face recognition in children and adults. *Developmental Science*, 6(1), 67–71.
- Hood, B. M., Willen, J. D., & Driver, J. (1998). Adults’ eyes trigger shifts of visual attention in human infants. *Psychological Science*, 9(2), 131–134.
- Hooker, C. I., Paller, K. A., Gitelman, D. R., Parrish, T. B., Mesulam, M. M., & Reber, P. J. (2003). Brain networks for analyzing eye gaze. *Brain Research. Cognitive Brain Research*, 17(2), 406–418.
- Janik, S. W., Wellens, A. R., Goldberg, M. L., & Dell’osso, L. F. (1978). Eyes as the center of focus in the visual examination of human faces. *Perceptual and Motor Skills*, 47(3 Pt 1), 857–858.

- Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, 6(10), 766–774.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17, 4302–4311.
- Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., et al. (1999). The human amygdala plays an important role in gaze monitoring. A PET study. *Brain*, 122(Pt 4), 779–783.
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, 4(4), 138–147.
- Klin, A., Jones, W., Schultz, R., Volkmar, F., & Cohen, D. (2002). Visual fixation patterns during viewing of naturalistic social situations as predictors of social competence in individuals with autism. *Archives of General Psychiatry*, 59(9), 809–816.
- Langdell, T. (1978). Recognition of faces: An approach to the study of autism. *Journal of Child Psychology and Psychiatry*, 19(3), 255–268.
- Langton, S. R. (2000). The mutual influence of gaze and head orientation in the analysis of social attention direction. *The Quarterly Journal of Experimental Psychology A*, 53(3), 825–845.
- Langton, S. R., & Bruce, V. (1999). Reflexive visual orienting in response to the social attention of others. *Visual Cognition*, 6(5), 541–567.
- Langton, S. R., Watt, R. J., & Bruce, I. I. (2000). Do the eyes have it? Cues to the direction of social attention. *Trends in Cognitive Sciences*, 4(2), 50–59.
- Laughery, K. R., Alexander, J. F., & Lane, A. B. (1971). Recognition of human faces: Effects of target exposure time, target position, pose position and type of photograph. *Journal of Applied Psychology*, 55, 477–483.
- Luria, S. M., & Strauss, M. S. (1978). Comparison of eye movements over faces in photographic positives and negatives. *Perception*, 7(3), 349–358.
- Macrae, C. N., Hood, B. M., Milne, A. B., Rowe, A. C., & Mason, M. F. (2002). Are you looking at me? Eye gaze and person perception. *Psychological Science*, 13(5), 460–464.
- Mah, L., Arnold, M. C., & Grafman, J. (2004). Impairment of social perception associated with lesions of the prefrontal cortex. *American Journal of Psychiatry*, 161(7), 1247–1255.
- Mansfield, E. M., Farroni, T., & Johnson, M. H. (2003). Does gaze perception facilitate overt orienting? *Visual Cognition*, 10(1), 7–14.
- Maurer, D. (1985). Infants' perception of facedness. In T. Field, & N. Fox (Eds.), *Social perception in infants* (pp. 73–100). Norwood, NJ: Ablex.
- McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, 9, 605–610.
- McKelvie, S. J. (1976). The role of eyes and mouth in the memory of a face. *American Journal of Psychology*, 89, 311–323.
- Ogai, M., Matsumoto, H., Suzuki, K., Ozawa, F., Fukuda, R., Uchiyama, I., et al. (2003). fMRI study of recognition of facial expressions in high-functioning autistic patients. *Neuroreport*, 14(4), 559–563.
- Pageler, N. M., Menon, V., Merin, N. M., Eliez, S., Brown, W. E., & Reiss, A. L. (2003). Effect of head orientation on gaze processing in fusiform gyrus and superior temporal sulcus. *Neuroimage*, 20(1), 318–329.
- Pelphrey, K. A., Sasson, N. J., Reznick, J. S., Paul, G., Goldman, B. D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*, 32(4), 249–261.
- Pelphrey, K. A., Singerman, J. D., Allison, T., & McCarthy, G. (2003). Brain activation evoked by perception of gaze shifts: The influence of context. *Neuropsychologia*, 41(2), 156–170.
- Perrett, D. I., Smith, P. A., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., et al. (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.
- Premack, D., & Woodruff, G. (1978). Chimpanzee problem-solving: A test for comprehension. *Science*, 202(4367), 532–535.
- Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience*, 18(6), 2188–2199.
- Ricciardelli, P., Bricolo, E., Aglioti, S. M., & Chelazzi, L. (2002). My eyes want to look where your eyes are looking: Exploring the tendency to imitate another individual's gaze. *Neuroreport*, 13(17), 2259–2264.
- Ristic, J., Mottson, L., Friesen, C. K., Iarocci, G., Burack, J. A., & Kingstone, A. (2005). Eyes are special but not for everyone: the case of autism. *Brain Research. Cognitive Brain Research*, 24(3), 715–718.
- Schultz, R. T., & Klin, A. (2002). Genetics of childhood disorders: XLIII. Autism, part 2: Neural foundations. *Journal of the American Academy of Child and Adolescent Psychiatry*, 41(10), 1259–1262.
- Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information. *Psychological Science*, 13(5), 402–409.
- Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. *Visual Cognition*, 12(1), 127–144.
- Sereno, A. B., Briand, K. A., Amador, S. C., & Szapitel, S. V. (2006). Disruption of reflexive attention and eye movements in an individual with a collicular lesion. *Journal of Clinical and Experimental Neuropsychology*, 28(1), 145–166.
- Stuss, D. T., Gallup, G. G., Jr., & Alexander, M. P. (2001). The frontal lobes are necessary for 'theory of mind'. *Brain*, 124(Pt 2), 279–286.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology*, 2, 225–245.
- Vecera, S. P., & Rizzo, M. (2006). Eye gaze does not produce reflexive shifts of attention: Evidence from frontal-lobe damage. *Neuropsychologia*, 44(1), 150–159.
- Vinette, C., Gosselin, F., & Schyns, P. (2004). Spatiotemporal dynamics of face recognition in a flash: It's in the eyes. *Cognitive Science*, 28, 289–301.
- Vuilleumier, P. (2002). Perceived gaze direction in faces and spatial attention: A study in patients with parietal damage and unilateral neglect. *Neuropsychologia*, 40(7), 1013–1026.
- Vuilleumier, P., George, N., Lister, V., Armony, J., & Driver, J. (2005). Effects of perceived mutual gaze and gender on face processing and recognition memory. *Visual Cognition*, 12(1), 85–101.
- Walker-Smith, G. J., Gale, A. G., & Findlay, J. M. (1977). Eye movement strategies involved in face perception. *Perception*, 6(3), 313–326.
- Wicker, B., Michel, F., Henaff, M. A., & Decety, J. (1998). Brain regions involved in the perception of gaze: A PET study. *Neuroimage*, 8(2), 221–227.
- Wicker, B., Perrett, D. I., Baron-Cohen, S., & Decety, J. (2003). Being the target of another's emotion: A PET study. *Neuropsychologia*, 41(2), 139–146.
- Yarbus, A. (1967). *Eye movements and vision*. New York: Plenum.
- Young, A. W., Aggleton, J. P., Hellawell, D. J., Johnson, M., Brooks, P., & Hanley, J. R. (1995). Face processing impairments after amygdalotomy. *Brain*, 118(Pt 1), 15–24.