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Effects of perceived mutual gaze and gender on face processing and recognition memory

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Perceived gaze contact in seen faces may convey important social signals. We examined whether gaze perception affects face processing during two tasks: Online gender judgement, and later incidental recognition memory. Individual faces were presented with eyes directed either straight towards the viewer or away, while these faces were seen in either frontal or three-quarters view. Participants were slower to make gender judgements for faces with direct versus averted eye gaze, but this effect was particularly pronounced for faces with opposite gender to the observer, and seen in three-quarters view. During subsequent surprise recognition-memory testing, recognition was better for faces previously seen with direct than averted gaze, again especially for the opposite gender to the observer. The effect of direct gaze was stronger in both tasks when the head was seen in three-quarters rather than in frontal view, consistent with the greater salience of perceived eye contact for deviated faces. However, in the memory test, face recognition was also relatively enhanced for faces of opposite gender in front views when their gaze was averted rather than direct. Together, these results indicate that perceived eye contact can interact with facial processing during gender judgements and recognition memory, even when gaze direction is task-irrelevant, and particularly for

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faces of opposite gender to the observer (an influence which controls for stimulus factors when considering observers of both genders). These findings appear consistent with recent neuroimaging evidence that social facial cues can modulate visual processing in cortical regions involved in face processing and memory, presumably via interconnections with brain systems specialized for gaze perception and social monitoring.

Face processing is one of the most complex visual skills of humans, providing rich and important information for social behaviour. Much research has been conducted on the specificity of visual processes involved in face perception, and there is now abundant evidence suggesting that face recognition may rely on highly specialized brain regions. Neuropsychological observations have long revealed that focal damage to inferior temporal cortex in humans can cause selective deficits in recognizing known faces and learning new faces (i.e., prosopagnosia; see Damasio, Tranel, & Damasio, 1990; Grüsser & Landis, 1991). Functional neuroimaging studies in healthy subjects have identified an area in fusiform cortex that can respond more strongly to faces than other classes of visual stimuli across a range of tasks and stimuli (Haxby, Hoffman, & Gobbini, 2000; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000). But face processing involves the extraction of many other important types of information from faces, in addition to a person's identity, including emotional expression, eye gaze direction, speech movements of the lips, and so on. The processing of these various facial cues can allow an observer to infer mental states, moods, or intentions, which may be crucial for communication and appropriate social interactions.

Findings in both healthy and brain-damaged subjects have suggested that these different types of facial information may be selectively processed in separable functional subsystems (Bruce & Young, 1986; Haxby et al., 2000), even though our subjective experience of seeing someone's face, and any inferences we might draw about their mental states or communicative intents, may involve some integration or interaction between the different types of perceived facial information In the present study, we examined how distinct facial properties related to enduring facial identity, or to more transient and changeable cues about gaze direction, may interact. We asked whether encoding of novel faces might be modulated by their perceived gaze (and head) direction, and whether this might also influence subsequent recognition memory for these faces. We also examined whether any such effect might depend on the relative genders (same or different) of the observer and the seen face (see below). Mutual eye contact can transmit socially important information about another person's intentions and interests, potentially signalling an upcoming social interaction, whether this be attraction leading to a friendly exchange, or threat leading to aggression (Campbell, Wallace, & Benson, 1996; Driver, Davis, Riciardelli, Kidd, Maxwell, & Baron-Cohen, 1999; Emery, 2000). It may therefore be crucial to detect whether we are being looked at or not (Gibson & Pick, 1963; Ricciardelli, Baylis, & Driver, 2000). Catching someone's eye implies that a direct social exchange might take place and could then elicit a more attentive analysis of the person's face, engaging the viewer in more active processing.

In the present experiment, we manipulated both eye gaze (direct or averted) and head orientation (frontal or three-quarters view) of unfamiliar faces while these were initially exposed for an online gender judgement task. We tested for any effect of eye gaze on such online judgments, as well as on subsequent incidental recognition memory. Recent functional imaging studies have revealed that direct eye gaze in seen faces, depicting mutual gaze contact with the observer, can increase activation in both amygdala (Kawashima et al., 1999) and fusiform cortex (George, Driver, & Dolan, 2001), but the behavioural consequences of such brain activations are still entirely unknown. Based on these findings, we predicted that faces might be remembered better when perceived gaze was directed towards versus away from the observer. We also wanted to assess whether any such effect might be more pronounced for direct gaze from faces seen in three-quarters view rather than frontal view (since seeing such a face might signal that the person has a more deliberate intention to look at the observer). In addition, if direct eye contact conveys any special affective and social meaning, one might ask whether any influence of perceived eye contact can differ as a function of the gender relationships between the viewer and the seen faces. Note that if male observers showed eye-contact effects more strongly for seen female faces than seen male faces, and vice versa, then any such effect could not be solely explained by stimulus factors alone, as this would depend on the observer's gender also.

Some recent behavioural findings have in fact already suggested that performance in both online face categorization task and face memory tasks can be influenced by seen gaze direction (Hood, Macrae, Cole-Davies, & Dias, 2003; Macrae, Hood, Milne, Rowe, & Mason, 2002), although these two studies did not systematically investigate any role of gender differences. Nor did these studies examine any effects of gaze direction when varied independently from seen head direction (unlike the fMRI study of George et al., 2001), even though seen head angle can modulate the perceived salience of gaze signals (Langton, Watt, & Bruce, 2000; Ricciardelli et al., 2000). Since seen head or body orientation may also reflect the direction of a person's attention, and can interact with the perception of eye gaze (Hietanen, 1999; Langton et al., 2000), it is possible that the previous findings obtained in tasks where eye direction was only changed for frontal views of faces (e.g., Hood et al., 2003; Macrae et al., 2002) might also be observed when head orientation is changed, irrespective of eye position, or that any eye gaze effects might be additively modulated by head orientation (i.e., being maximal when both eyes and head are straight). Note also that direct gaze in frontal views of faces is exceptional in providing a symmetrical image, which does not apply for direct gaze from any other seen head angle (e.g., see George et al., 2001). Finally, the meaning of perceived gaze direction may also interact with affective values (Adams, Gordon, Baird, Ambady, & Kleck, 2003) and attractiveness (Kampe, Frith, Dolan, & Frith, 2001), and results from social psychology suggest that person perception can be strongly influenced by facial information about gender category (Macrae et al., 2001). We therefore sought also to test for any influence of the gender relationship between seen faces and observers on the impact of direct or indirect gaze—a question not addressed hitherto.

METHOD

The 22 participants (11 males, 11 females) were healthy paid volunteers, ranging from 18 to 30 years: mean 22.1 years for females and 23.4 years for males; unpaired *t*-test, $t(20) = 1.31$, $p = .21$. They sat ~50 cm in front of a computer screen on which static greyscale digitized photographs of faces (~8° × 12°) were shown on a grey background. All face stimuli (32 male and 32 female) involved individuals unknown to our participants and were systematically taken under the same lightning and position conditions. In order to distinguish between any effects of direct eye gaze *per se*, versus other aspects of the face (e.g., near-symmetry of the image only for direct gaze in frontal views of faces), we used four different types of stimuli (see George et al.'s, 2001 fMRI study) in which the direction of eyes (straight towards the camera/observer, or averted by 30°) and head position (straight or rotated by 30° from the camera/observer) were manipulated independently in a 2 × 2 factorial design (Figure 1). Thus, when collapsing over rightwards and leftwards direction of deviation (half each), there were four possible types of stimuli: Straight head with straight eyes; straight head with averted eyes; averted head with straight eyes; and averted head with averted eyes (always both averted towards the same side in the latter condition).

The experiment comprised a first exposure phase and a subsequent memory phase, given in the same session. In phase 1 (exposure), participants were presented with 32 different faces in turn, in randomized order. Half were male, half female in an intermingled sequence (and thus half matched or did not match the gender of the observer, which was also equally likely to be male or female for different participants, due to the two subgroups of 11 participants). Half of the faces were gazing direct at the viewer (eyes ''straight'' in this sense, but note that the seen eye stimuli are then very different for frontal or three-quarters views of faces; see Figure 1) and half were gazing away from the viewer (rightwards or leftwards averted, equally probable). In each of these conditions, half had the head directly facing the viewer (frontal view) and half had the head

Figure 1. Examples of the four possible types of stimuli. Eye direction (towards or away from the camera/observer) and head direction (again towards or away) were independently manipulated. Note that the eye region is visually very different for direct gaze in a deviated or frontal face.

averted (three-quarters rightwards or leftwards, equally probable), resulting in four different stimulus conditions in total (Figure 1). All stimuli were randomly mixed and counterbalanced across subjects. Participants were asked to classify the faces as male or female as quickly as possible by pressing one of two keys, and were not told that their memory would subsequently be tested. Each trial began with a central fixation point appearing at the centre of screen for 1 s, followed by a face for 3 s. Then, a blank delay of 1 s preceded the fixation stimulus for the next trial.

Phase 2 (memory test) followed after a short 1 min unfilled break. Participants were shown 64 faces presented each in turn, half of which had been seen before (‘‘old’’) and half being foils (‘‘new’’), with particular stimuli counterbalanced across participants. The four conditions above (i.e., including the two possible eye directions crossed with the two possible head positions; see Figure 1), plus male or female gender, were all equally probable for both ‘‘old’’ faces (all presented under the same display conditions as in phase 1) and for ‘‘new’’ faces. The stimuli were randomly mixed, in a different order across subjects. The task now was a forced-choice decision (‘‘yes’’/’’no’’) as to whether or not the face currently shown had been exposed in the preceding study phase. Each face stimulus remained visible until a response was made.

Note that in both phases of the experiment, eye gaze and head direction were entirely irrelevant to the task of either gender classification, or old/new classification.

RESULTS

Exposure phase

Mean error rates and correct response times for judging gender of the faces were computed for each participant and submitted to a mixed-design ANOVA. Eye gaze (straight or averted), head position (frontal or three-quarters view), and gender match of each face stimulus with respect to the participant (opposite or same) constituted within-subject factors, whereas gender of the participant was also taken into account as a between-subject factor. Participants made very few errors (mean proportions 0.11 ± 0.31), without any difference between gaze conditions, $F(1,20) < 1.69$, $p > .21$. Error rate was not affected by the gender match of faces, $F(1,20) = 0.63$, but was higher in male than female participants (mean 0.15 ± 0.21 and 0.07 ± 0.37, respectively), $F(1,20) = 4.68$, $p = .044$.

More critically, RTs for judging face gender were significantly influenced by the direction of eye gaze in the seen faces, with this influence also being modulated by seen head direction, as well as by the match between the participants' and the faces' gender (Figure 2). The main effect of eye direction was only marginally significant in a mixed ANOVA, $F(1,20) = 3.19$, $p = .089$, although across all other conditions RTs were generally slower for faces with eyes directed to the observer, as compared with eyes averted (mean 1055 vs. 1007 ms). These slower RTs for gender judgements in the presence of perceived eye contact were modulated by a significant two-way interaction with head position, on the one hand, $F(1,20) = 4.62$, $p = .044$, and a two-way interaction with gender match, on the other hand, $F(1,20) = 7.69$, $p = .012$. Thus, responses were significantly slower for faces with direct versus averted eye gaze when their head direction was averted (1072 vs. 983 ms), $t(43) = 2.53$, $p = .015$, but not when the face was seen in frontal view (1036 vs. 1031 ms), $t(43) = 0.13$ (see Figure 2a). The main effect of head position was not significant, $F(1,20) = 0.5$.

In keeping with the Eye gaze × Gender match interaction above, responses were particularly delayed by direct versus averted eye gaze when male participants judged a female face (mean 845 vs. 722 ms), $t(21) = 2.21$, $p = .038$, or when female participants judged a male face (1391 vs. 1276 ms), $t(21) = 2.38$, $p = .027$, but there was no reliable effect of eye direction when male participants judged male faces or female participants judged female faces, $t(21) < 1.42$, $p > .17$. Thus, the main effect of eye direction was highly significant when considering only faces with gender opposite to the participant, $F(1,0) = 7.45$, $p = .012$, but not when considering faces with same gender, $F(1,20) = 0.66$. These longer RTs associated with perceived gaze contact for faces of opposite gender were found in both male and female participants (Figure 2b), without any higher level interaction involving the participants' own gender, $F(1,20) < 0.5$. Likewise there was no triple interaction between eye direction, head direction, and gender match, $F(1,20) = 0.14$. A general trend for faster responses in male than female

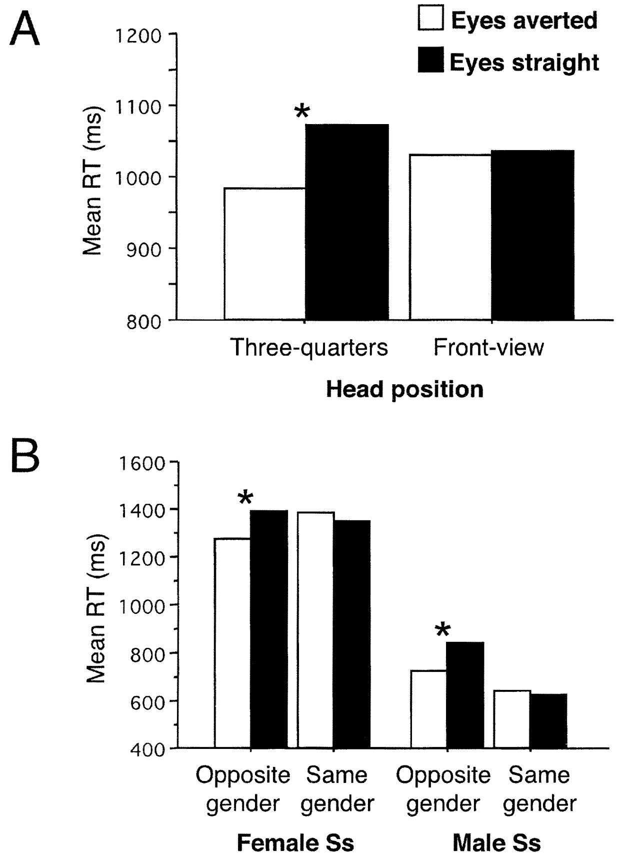

Figure 2. Effects of seen gaze-direction on RTs for face gender decisions. Seen eye-contact led to longer RTs selectively for (A) faces in three-quarters views, and for (B) faces with gender opposite to the observer (B). $^*p < .05$.

participants failed to reach significance, $F(1,20) = 2.81$, $p = .11$. No other terms were significant.

These data suggest that the speed of face processing during gender judgements was influenced conjointly by the perceived gaze contact with seen faces, and by the mismatch with the participant's own gender, even though neither of these two properties were directly relevant to the prescribed task.

Memory phase

The rate of correct hits and correct rejections during the recognition-memory test, as well as RTs, were computed for each participant and each condition. These data were analysed by mixed ANOVA, using the two possible eye-gaze directions (direct or averted), head direction (frontal or three-quarters view), gender of each face stimulus with respect to the observer (opposite or same), and stimulus memory condition (old or new foil), as within-subject factors. In addition, gender of the observer (regardless of the seen face) was again taken into account as between-subject factor.

For accuracy data, the main effect of the old/new stimulus condition showed no significant difference between the rate of correct responses for ‘‘old’’ versus ‘‘new’’ faces, $F(1, 0) = 0.78$, $p = .38$. Overall, participants produced correct ‘‘old’’ responses for 71.2% of previously exposed faces and correct ‘‘new’’ responses for 75.2% of novel foil faces. However, performance was again significantly affected by gaze direction, head direction, and gender mismatch between the seen face and the observer.

There was a main effect of head direction, $F(1, 20) = 2.73$, $p = .006$, with a higher rate of correct responses for faces seen in three-quarters rather than frontal view, for both ‘‘old’’ (74.6% vs. 68.7% correct) and ‘‘new’’ (77.3% vs. 73.2% correct) stimuli, regardless of their eye position and gender (all Fs < 0.65 for those interactions). Such an advantage of three-quarters views of faces has commonly been reported in other recognition studies (Blanz, Tarr, & Bülthoff, 1999; Bruce, Valentine, & Baddeley, 1987).

There was no main effect of eye direction alone since memory showed only a very slight tendency to be better overall for faces with straight compared to averted eye gaze (73.6% vs. 72.8% correct), but without even approaching significance, $F(1, 0) = 0.31$. The more critical findings concerned a significant three-way interaction of the old/new factor with eye gaze direction and head direction, $F(1, 20) = 5.81$, $p = .025$, as well as a four-way interaction of old/new with eye gaze, head direction, and mismatch between the participant’s gender and that of the seen face, $F(1, 20) = 5.29$, $p = .032$.

One source for these interactions was that the effects of eye direction and head direction on performance were specifically found when considering the rate of correct hit responses recognition to ‘‘old’’ faces, $F(1, 20) > 5.13$, $p < .035$ for the three-way and four-way interactions, but not when considering the rate of correct rejections for ‘‘new’’ faces, $F(1, 20) > 2.23$, $p = .15$ for the same interactions. This is consistent with a genuine effect of direct gaze in deviated heads on improving memory for old stimuli, rather simply inducing a response bias for different stimulus types during the old/new judgement, regardless of actual memory. Thus, ‘‘old’’ faces seen in three-quarters view were much better recognized as having previously been exposed when having direct rather than averted gaze (77.9% vs. 64.7%), paired t-test, $t(43) = 2.91$, $p = .006$; whereas in contrast there was no significant effect of eye direction for frontal-view ‘‘old’’ faces, $t(43) = 1.68$, $p = .10$.

In addition, the significant four-way interaction also reflected an improved recognition of three-quarters faces with straight eye gaze specifically when participants judged faces of opposite gender, i.e., when male participants judged female faces or female participants judged male faces, $F(1, 20) = 15.01, p = .001$, for this direct eye-gaze advantage in three-quarters faces with opposite sex (see Figure 3b). By contrast, recognition of frontal faces tended to be enhanced by averted rather than direct gaze, again especially when the faces' gender was opposite to the participants' own gender, $F(1, 20) = 4.60, p = .044$ for this averted-gaze advantage in front-view faces with opposite sex. Both of these effects were similar in male and female participants (no interactions involving the observers' own gender, rather than their gender relationship to the seen face, reached significance; all $F(1, 20) < 2.5$, all $p > .12$). No other terms were significant.

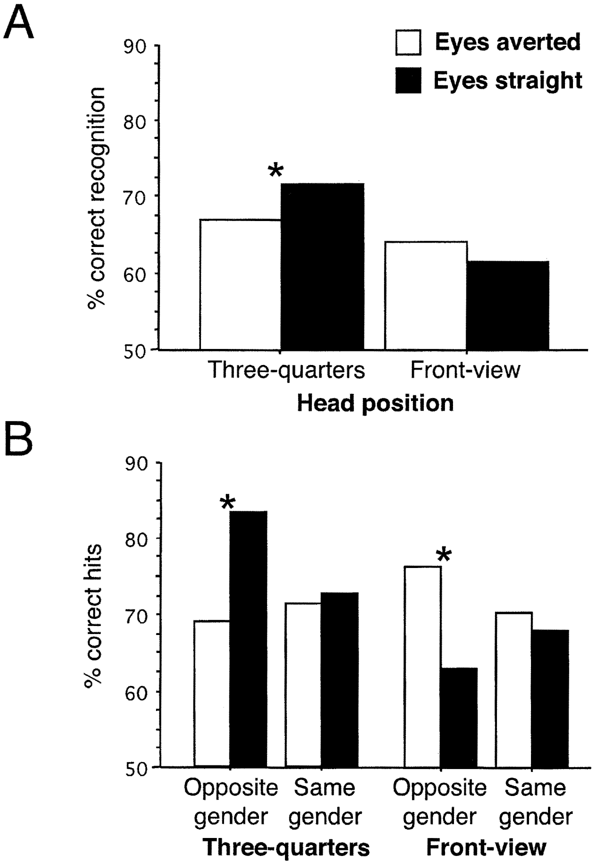

Figure 3. Effect of seen gaze-direction on recognition memory for faces. (A) Mean accuracy (percentage of correct recognition for old faces and correct rejections for new faces) was higher for faces with gaze directed to the observer than with averted gaze, specifically when faces were shown in a three-quarters view. (B) Effects of gaze occurred mainly on correct recognition of old faces whose gender was opposite to the participants. $*p < .05$.

These data again suggest influences of seen gaze direction on performance in a face-judgement task (now recognition memory), with a consistent modulation involving gaze direction, head direction, and gender mismatch between seen faces and observers. Recognition memory was especially better for three-quarters views of faces with direct gaze, but particularly so for the opposite gender to the observer.

DISCUSSION

Our results indicate that perceived eye contact can affect both the speed of online face judgements (here for gender) and the subsequent accuracy of incidental recognition memory for previously unknown faces. We found that direct gaze can lead to slower gender judgements, and modulate subsequent face recognition in a surprise memory test, particularly when faces appear with direct gaze towards the observer but are seen in a three-quarters view. Furthermore, these influences of eye contact with deviated faces were consistently modulated by whether the seen faces had the opposite gender to that of the observer, rather than the same gender. Note that this influence cannot be attributed to aspects of just the stimuli themselves (such as, say, three-quarters views of faces with direct gaze somehow exposing more information about eye shape than other combinations), since the stimuli were held constant across male and female observers, with the effect of gender mismatch depending on the gender relationship between the observer and the seen face, not just the stimulus itself. Thus, faces were not only counterbalanced across conditions in different participants but also counterbalanced between genders. Taken together, our various findings demonstrate that gaze information can significantly interact with processing of other facial attributes.

During the initial exposure phase, response times were longer for three-quarters views of faces with gaze directed towards the observer, and also prolonged for faces with opposite gender. Thus, male participants took longer to judge the gender of female three-quarters views of faces with straight compared to averted eyes, whereas female participants conversely took longer to respond to male faces with straight versus averted eyes. Moreover, during the subsequent memory test, recognition for a given person's face was enhanced when eye gaze was directed towards the observer, rather than directed away, specifically when the head was in a three-quarters view (in contrast frontal faces tended to be better recognized with their eyes directed away). This effect was again stronger for faces whose gender was opposite to that of the observer.

Importantly, these effects of seen gaze occurred despite the fact that eye direction in faces was not explicitly relevant to the prescribed task during either the first exposure phase or the subsequent memory test. This might suggest that the influence of seen gaze on face processing, and the enhancement of subsequent recognition memory, can occur through mechanisms that operate in a largely involuntary and automatic manner, possibly independent of the observer's explicit task. Such an influence may be consistent with proposals that seen gaze direction provides a crucial social signal that may receive dedicated processing in the visual system of primates (Perrett, Rolls, & Caan, 1982; Perrett et al., 1985), and might exert significant influences on highly specialized mechanisms for social attention and behaviour (Brothers & Ring, 1993; Driver et al., 1999; Vuilleumier, 2002). However, further research is needed to determine to what extent the effects observed here are fully automatic, or might instead reflect incidental ''evaluation'' routine that might operate spontaneously under conditions of relatively easy or ''low-load'' task, yet might still be modulated (e.g., suppressed or enhanced) to some extent as a function of explicit task requirements (being reduced, say, when observers must judge nonfacial attributes and thus ignore a face in sight; or being enhanced when observers must explicitly judge potentially related social properties, such as attractiveness or trustworthiness).

Detecting direct eye contact from seen faces has obvious significance for guiding adequate social communication and behavioural response, as this can potentially signal that another creature has a particular interest or intention concerning the viewer, either bad (e.g., if you are potential prey) or good (e.g., if you are a potential collaborator or mate). Humans are highly sensitive in monitoring the gaze direction of other people, and may effectively use and interpret direct gaze as an expression of various interpersonal attitudes, such as aggression or dominance, friendliness or seduction, as well as nonverbal signals for regulating conversation (Argyle & Cook, 1976; Emery, 2000; Gibson & Pick, 1963; von Grünau & Anston, 1995). It may therefore be expected that perceived eye contact from a seen face should engage the observer's attention, and thus enhance processing of that person's face. Such enhancement of face processing might underlie the prolonged analysis (reflected by longer response times) for faces with direct gaze, as we found for gender judgements during the initial exposure phase. It may also subsequently lead to better recognition memory for such faces, as we found during the memory test phase. Furthermore, the fact that our effects were generally greater for faces of an opposite gender to the observer may be consistent with proposals that gaze analysis is particularly important in relation to such socially significant factors (Kampe et al., 2001; Langton et al., 2000; Perrett et al., 1990).

Our results for the first exposure-phase might appear partly at odds with a recent study (Macrae et al., 2002) reporting *faster* response times in a gender categorization task when faces were shown with direct eye gaze (versus averted), and no difference between three-quarters and front views. However, that study (Macrae et al., 2002) did not examine the effects of gender mismatch between seen faces and observers, which was found to be the critical factor here. Moreover, their study did not include a condition with both head and eyes averted, so it could not test for any interactions of Eye × Head direction as we found here. It is also possible that cropping of the stimuli used in their study but not ours may have changed the categorization strategy used by their subjects (Goshen-Gottstein & Ganel, 2000). In addition, average RTs were much faster overall in Macrae et al. (2002) than in our study (i.e., around 600 ms vs. 1000 ms when collapsing across all conditions), which might reflect several potential differences in the task such as a greater difficulty of stimulus discrimination, absence of strong emphasis on speeded response, and a prolonged fixed exposure duration for each face in our study (to allow reliable encoding and avoid exposure differences for subsequent memory test). In any case, further research is needed to clarify the origin of these differences, although note that the present influences of gender mismatch were found here in both the exposure phase and the subsequent test of recognition memory.

Moreover, our results from the subsequent memory phase converge nicely with another study (Hood et al., 2003) where enhanced memory was found for frontal views of faces presented with direct versus averted eyes either at encoding or at retrieval. However, since the latter study did not manipulate gaze direction and head direction independently, in a fully 2 × 2 factorial design as here, it could not rule out explanations due to potential differences in the basic visual properties of the stimuli used (e.g., symmetry, which exists only for frontal views of faces with direct gaze; see George et al., 2001). In the current study, we found that the effects of direct gaze towards the observer were consistently stronger when head direction was averted (i.e., in three-quarters views of the faces), rather than frontal, both during gender judgement and during recognition memory. Moreover, our effects of gender mismatch between the seen face and the observer cannot be attributed to stimulus factors alone, since particular face stimuli were counterbalanced across the participant subgroups, as noted above.

It is noteworthy that perceived eye contact seems especially salient to the observer in a seen face that has an averted head direction (as readers can note for themselves by inspecting Figure 1), possibly because the incongruity between head direction and eye gaze emphasizes the directional intent of the gaze (and perhaps even some effort of the observed person). In contrast, straight gaze in a straight (frontal view of) a head may constitute a more ''ordinary'' posture, with eyes occupying this position by default rather than manifestly focusing in the direction of the observer, therefore arguably producing less effect on mechanisms of social attention. By contrast, for a deviated head the expected default posture for the seen face might be correspondingly deviated gaze, so that when gaze is directed instead towards the observer in a deviated face, this becomes more salient to the observer. On the other hand, averted gaze in faces with a straight head resulted in better recognition, as compared with straight gaze, presumably because of the greater salience and greater social information potentially associated with this situation. The present modulations of the effect of eye contact as a function of head rotation may be consistent with other behavioural findings (e.g., Hietanen, 1999, 2002; Langton et al., 2000; but see Anstis et al., 1969) showing that gaze direction may be integrated with other cues from seen head and body position for the processing of another person's attention and intentions. In keeping with this, some neurophysiological findings (Perret et al., 1990; Perrett, Hietanen, Oram, & Benson, 1992) have been taken to suggest that neurons in STS may implement ''direction-of-attention'' detectors (DADs) combining information from eye direction, head orientation, and body position through reciprocal interconnections between different neuronal populations. Our results extend previous behavioural findings in humans on integration of eye and head cues in gaze perception, to suggest that these may interact with basic processing of facial identity, such as gender judgement and recognition memory tasks, even when gaze direction is not relevant to the task demands.

We should note that, in addition to direct gaze in three-quarters views of faces yielding better recognition memory, averted gaze in frontal views of faces also tended to result in better recognition than direct gaze. This pattern of strongly enhanced memory for deviated head with direct gaze, but also some enhancement for frontal views of faces with averted gaze, might reflect a more general sensitivity to some incongruence between head and eye direction (since it is probably more natural to keep both aligned, see discussion of ''default'' postures above). Such incongruence itself might constitute an important cue for systems processing faces and social signals, alerting to a potentially unusual or behaviourally relevant encounter. Indeed, one might consider whether the ''novelty'' or relative infrequency of a seen head/gaze combination might have some influence on performance, although note that for this to play any role in explaining the gender mismatch effects that we observed, it would have to be the case that direct gaze from males with deviated faces towards females (and equally from females with deviated faces towards men) is less commonly seen than for matching gender situations.

Taken together, our data provide evidence that perceived eye contact can influence other aspects of face processing, even for a single exposure of an unfamiliar face. In addition to such influences at initial encoding, some effect of seen gaze might possibly also occur at retrieval, during the recognition test phase (Hood et al., 2003). This cannot be entirely ruled out for the memory results in our study, since the same photographs (i.e., with identical gaze, and head direction) were shown here during both the exposure and the recognition phases. However, note that this similarity between exposure and test applied to all types of faces, with a selective modulation by gaze found only in some conditions (i.e., particularly in three-quarters views of opposite-gender faces with direct gaze towards the observer), over and above the repetition of the same photograph. Note also that the critical memory effects were found only for ''old'' previously exposed stimuli, not as response biases applying equally to new ''foil'' stimuli.

Several previous studies have shown significant effects of seen gaze direction on spatial shifts of attention, speeding detection of events occurring at the locations being looked at by task-irrelevant faces (e.g., Driver et al., 1999; Friesen & Kingstone, 1998; Vuilleumier, 2002), providing another demonstration that social gaze cues in faces can influence visual perception and behaviour. But it seems unlikely that the effects of seen gaze direction on face memory in our study could be explained by attention being shifted away from faces with averted gaze, leading to worse subsequent memory for the latter, rather than better memory for faces with direct gaze. First, memory for frontal views of faces was actually better with averted than direct gaze, when there was a gender mismatch. Second, reflexive shifts in attention due to seen averted gaze are thought to be fast and transient, lasting a few hundreds of milliseconds at most, so seem unlikely to significantly disrupt face processing in our study, where each face was presented for 3 s during the initial exposure and for an unlimited time until response during the memory test. Finally, any influence from systematic shifts in attention away from a face due to its averted gaze should have led to longer response times than for faces with direct gaze, whereas we actually found the opposite pattern under the present experimental conditions.

In keeping with our behavioural findings, a recent fMRI study (George et al., 2001) revealed enhanced visual responses in fusiform cortex for faces with direct compared to averted gaze during a gender judgement task. This study manipulated gaze direction and head position in a 2 × 2 factorial design, exactly as in the present behavioural experiment, and found that faces with direct gaze (relative to faces with averted gaze) produced a stronger activation in face-sensitive areas of fusiform cortex. It was suggested that the stronger fusiform activity evoked by faces with direct gaze might be due to enhanced attention and deeper encoding of these more salient stimuli, consistent with our present findings and proposals. Other neuroimaging studies have shown increased responses in visual cortex to faces gazing either straight to or away from the viewer, relative to faces with static or closed eyes (Wicker, Michel, Henaff, & Decety, 1998), not only in posterior superior temporal sulcus (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998), but also in several other extrastriate regions of occipital, inferotemporal, and parietal cortex (Wicker et al., 1998). Such effects seem consistent with enhanced attention to seen face-images that may tap into mechanisms concerned with potential social significance. George et al. (2001) also performed an analysis of functional ‘‘connectivity’’ between brain areas, showing that activity in fusiform cortex not only increased to faces with direct gaze, but also exhibited a greater coupling with activity in the amygdala for perceived eye contact. Another study using PET (Kawashima et al., 1999) found that the amygdala (a structure well-known to play a role in some forms of memory) was selectively activated by mutual gaze contact in faces shown on a video display, as compared with averted gaze. Notably, this effect was obtained with three-quarters views of faces that were very similar to our three-quarters condition, which led to the most enhanced memory during eye contact.

The amygdala is critically involved in processing the social and affective significance of environmental stimuli (Leonard, Rolls, Wilson, & Baylis, 1985), as well as in enhancing memory for affectively loaded events (Cahill, 1996). Damage to the amygdala in humans may impair perception of gaze direction (Young, Aggleton, Hellawell, Johnson, Broks, & Hanley, 1995). Such damage to the amygdala can also impair learning of newly encountered faces (Crane & Milner, 2002; Young et al., 1995), even without damage to the fusiform regions that have typically been associated with prosopagnosia. Taken together, these different lines of evidence suggest that gaze processing influences on the amygdala might serve to enhance perceptual analysis (e.g., in fusiform cortex) and memory formation for faces that convey affectively and socially salient signals (e.g., by feedback modulatory projections; see Amaral, Price, Pitkänen, & Carmichael, 1992; Iwai & Yukie, 1987). This would be consistent with the existence of prominent projections feeding back from the amygdala to fusiform cortex (Amaral et al., 1992; Iwai & Yukie, 1987) and greater functional coupling between amygdala and fusiform shown by neuroimaging studies for faces with direct versus averted gaze (George et al., 2001) or emotional versus neutral expression (Morris, Friston, Buchel, Frith, Young, Calder, & Dolan, 1998). A modulation of face processing in fusiform cortex by the amygdala, in response to perceived gaze contact (George et al., 2001) might thus provide a plausible substrate for the deeper encoding of faces with direct gaze, and better subsequent memory, as found in the current behavioural experiment. Our findings may therefore reflect the behavioural consequence of the observed increase in fusiform activity, and associated increases in amygdala activity or functional connectivity, as apparently elicited by faces with straight gaze in fMRI studies.

In summary, our findings indicate that seen gaze direction can modulate how faces are processed and then later remembered, in combination with seen head direction (the most pronounced effects for direct gaze being produced by deviated faces) as well as with other social factors such as gender relations (direct gaze from deviated face of opposite gender to the observer having the biggest effects). Models of face processing in cognitive neuroscience have typically emphasized the fact that gaze cues are processed by specialized neural subsystems that are functionally and anatomically distinct from subsystems involved in processing other information in faces, such as gender or identity (Bruce & Young, 1986). The present results may imply significant interactions between components of this distributed cerebral network for face perception (Breen, Caine, & Coltheart, 2000; Haxby et al., 2000), presumably involving a dynamic interplay between those areas concerned with the extraction of invariant facial traits (e.g., identity, gender) and those responding to variant properties (current head angle and gaze direction) of the seen person, which may send important social signals about that person's current interests or intentions.

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