
Trends Cogn. Sci. March 2009 Vol. 13 No. 3, pp. 101–144 ISSN 1364-6613
Trends in Cognitive Sciences
Focus on gaze and social attention
Mirror neurons and speech perception
The allocation of attention in reading
Forgetting in verbal short-term memory
Cell PRESS

Review

# Neural mechanisms of social attention

Lauri Nummenmaa[1,2] and Andrew J. Calder[3]

[1] Department of Psychology, University of Tampere, Biokatu 6, FIN-33014 Tampere, Finland
[2] Department of Psychology, University of Turku, Assistentinkatu 7, FIN-20014 Turku, Finland
[3] Medical Research Council, Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge CB2 7EF, UK

**Social attention is conveyed primarily by gaze, but also by head and body orientation. These cues not only signal a seen agent's direction of attention but are also used to infer their current goals and intentions. Here, we review recent research showing that different gaze, head and body orientations are represented by distinct neural mechanisms, and show that a statistical summary of recent neuroimaging studies reveals a widespread neural network for gaze processing. We discuss how this network subserves visual analysis of social attention cues, and imitative attention shifts and mental state attributions from these cues. We also review new research indicating that the posterior superior temporal sulcus region responds to the inferred intentionality of social cues, and consider the development of the gaze perception system.**

## Introduction

Humans possess remarkable social attention skills. From other people's eye gaze, head and body orientation we readily detect their focus of attention, orient our own attention to the same location and draw social-cognitive inferences regarding their goals, intentions and actions. These processes contribute to 'social attention' and have been the focus of a large body of studies in recent years addressing their functional and neural bases. We review recent advances in our understanding of the mechanisms of social attention, with a focus on gaze perception – the most salient and commonly investigated cue. First, we discuss the visual representation of different gaze, head and body orientations. We then present a quantitative analysis of human functional neuroimaging studies of gaze processing. This analysis reveals a widespread neural topography extending well beyond the superior temporal sulcus (STS), which has been the focus of the majority of studies. Next, we discuss brain mechanisms involved in drawing socio-cognitive inferences from gaze, and then briefly consider the development of the social attention system and its malfunction in autism spectrum conditions (ASC) (see Glossary). We conclude that social attention involves a more extensive neural network than originally assumed, incorporating areas involved in face perception, gaze perception, attention, emotion and mental state attribution. In addition, recent research calls for a re-evaluation of the role of the STS in gaze perception.

## Separable coding of different gaze, head and body directions

Seminal work by Perrett and others (Box 1) identified face-responsive neurons in the anterior STS (anterior superior temporal polysensory area, STPa) of monkeys tuned to different gaze, head and body orientations [1,2]. Over 20 years later, similar forms of separable coding in humans have been demonstrated using adaptation paradigms [3–5]. Adaptation has been primarily associated with low-level perceptual properties (e.g. colour [6], orientation and motion [7]), but recent evidence shows that complex objects, including faces, are also susceptible to these effects [8]. In the case of gaze, prolonged exposure (i.e. adaptation) to a series of faces gazing 25° left (or right) increases participants' tendency to perceive 5° and 10° gaze in the adapted direction as looking directly at them, whereas gaze in the opposite direction is unaffected or less likely to be perceived as direct [3,9,10] (Figure 1a). These effects persist over changes in the identity, size and head orientation of the adapting and probe faces [3], indicating that they are unlikely to reflect adaptation of low-level visual properties. Rather, we conclude that they demonstrate identity-invariant coding of gaze directions in humans.

### Glossary

**Adaptation**: a neural system's temporary reduction in responsiveness to a stimulus (often accompanied by a change in its perception) after prolonged exposure to the stimulus.
**Autism spectrum conditions (ASC)**: pervasive neurodevelopmental disorders characterized by widespread abnormalities of social interactions and communication, in addition to severely restricted interests and highly repetitive behaviour.
**Gaze following**: the process of following others' direction of attention from their gaze direction.
**fMRI-adaptation**: an fMRI design that employs adaptation, which can be used to study the response properties of sub-populations of neurons that might reside within the same unit (voxel) of a fMR image. In the context of functional imaging, adaptation is defined as a reduction in the BOLD signal after repeated presentation of identical stimuli. By changing different properties of the stimuli, and measuring the subsequent increase or decrease in the BOLD signal, one is able to probe the properties of the underlying cortical representation. See Ref. [16] for discussion of the possible neural mechanisms and models accounting for fMRIa.
**Joint attention**: sharing a common focus of attention such as an object or a spatial location with another individual.
**Multichannel coding**: representational framework comprising multiple channels (or cell populations) tuned to different stimulus features (e.g., left, direct and right gaze). The relative activation of the channels defines the actual percept.
**Opponent-coding**: representational framework in which a specific stimulus feature is represented by two cell populations broadly tuned to opposite ends of a continuum. The relative activation of the cell populations defines the percept, with equal engagement of the populations representing the intermediate state.
**Theory of mind**: social-cognitive processes that enable attribution of mental states such as intentions, desires and attitudes to other individuals.

---

*Corresponding author:* Nummenmaa, L. (lauri.nummenmaa@uta.fi).

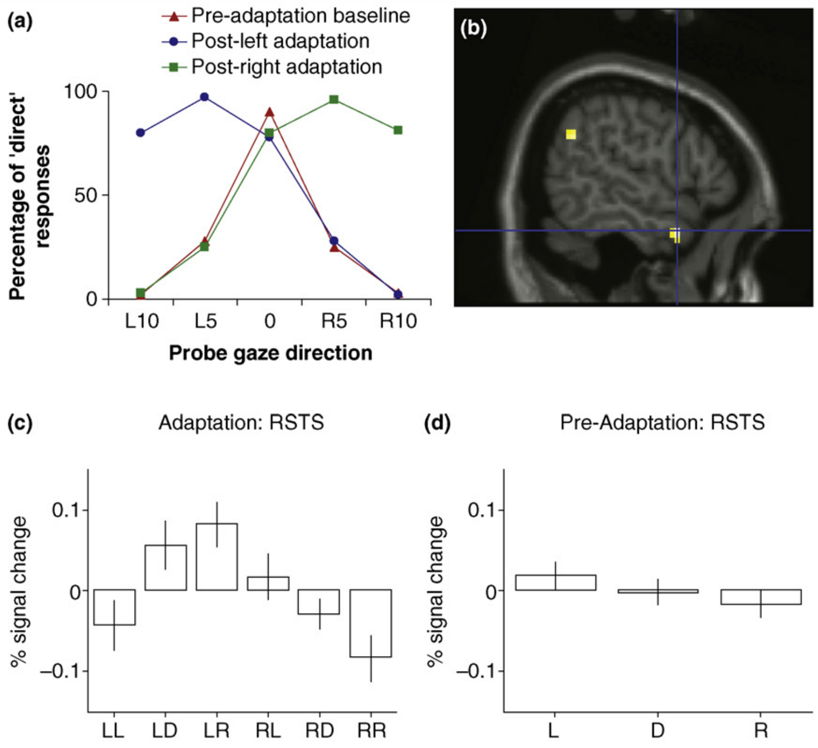
1364-6613/$ – see front matter © 2008 Elsevier Ltd. All rights reserved. doi:10.1016/j.tics.2008.12.006 Available online 14 February 2009

### Box 1. Electrophysiological recordings in macaques

Single-cell recording studies in macaques have identified face-selective neurons in the STPa. A small proportion showed a preferential response to particular faces but the majority were identity-invariant and showed relatively broad tuning to prototypical views of seen head orientations (full-face, left, right, both profiles, back-of-the-head and both head-up and head-down) [63]. A substantially smaller body of work found identity-invariant neurons coding eye gaze directions [2,63,64] and body orientations [15]. Notably, a large proportion of cells were responsive to the same direction signalled by gaze, head or body orientation, leading to the conclusion that they code others' direction of attention or 'social attention' [2]. These cells also showed a hierarchical preference responding primarily to the direction signalled by the gaze, followed by the head and then body orientation [2]; an order that represents the most to least reliable cue to where a person is attending. It is unclear whether a similar hierarchy exists in humans. Initial work showed that judgements of head and gaze direction demonstrate symmetrical interference for incongruent gaze-head pairings [65]; however, these effects are likely to depend on multiple factors, including angle of gaze deviation, temporal constraints on judgements and the relative contribution of different features outside the eye region [66].

Adaptation effects are often described in terms of two representational frameworks – opponent coding and multichannel coding. The coding of facial identify is optimally accounted for by an opponent-coding framework [11]. In contrast, single cell recordings in monkeys indicate that gaze is represented by a multichannel system, with separate channels (or cell populations) coding different gaze directions (e.g. left, direct, right). Calder *et al.* [10] provided support for mutichannel coding of gaze in additional adaptation research in humans; thus, facial identity and gaze are coded by distinct representational frameworks. This distinction is further supported by electroencephalographic (EEG) recordings showing that gaze adaptation influences event-related potentials (ERPs) substantially later (250–350 ms) [12] than facial identity adaptation, which affects the face-selective N170 ERP component [13]. Hence, despite the significant sensitivity of the N170 to the eyes [14], separable coding of different gaze directions is not manifested in this early face-sensitive response.

Additional work has shown that different orientations of heads [5] and bodies (with heads masked) [4] can also be selectively adapted, and that again, multichannel coding provides the optimal representational framework [4]. Consistent with gaze, these effects persist over changes in the identity of the adaptation and test stimuli, mirroring cell recording studies in monkeys showing identity-invariant coding of different gaze, head and body orientations [2,15]. Because these cells were found in the anterior STS, it is of particular interest that work using adaptation in combination with functional magnetic resonance imaging (fMRI-adaptation, [16]) has demonstrated separate cell populations coding identity-invariant representations of



TRENDS in Cognitive Sciences

**Figure 1**. The eye gaze aftereffect. **(a)** Prolonged exposure (i.e. adaptation) to 25° left or right gaze increases the tendency to perceive small angles of gaze (5° and 10°) in the adapted direction as direct gaze. By contrast, perception of gaze at the opposite direction is unaffected, or shows a decreased tendency to be perceived as direct [3]. These effects are found despite changes in size and head orientation between the adaptor and probe stimuli, and are consistent with separable neural coding of different gaze directions. L10 = 10° left gaze, L5 = 5° left gaze and so on. **(b)** fMRI-adaptation reveals that the anterior portion of the STS contains cells tuned to different directions of eye gaze [9]. **(c)** Following adaptation to 25° left (or right) gaze, responses of this region are greater for 10° gaze in the non-adapted versus adapted direction, with direct gaze resulting in an intermediate response. LL = left adaptation, left probe, LD = left adaptation, direct probe and so on. **(d)** By contrast, before adaptation, left, direct and right gaze probes produced equivalent responses. L = left gaze, D = direct gaze, R = right gaze. (a) Adapted, with permission, from Ref. [3]. (b–d) Adapted, with permission, from Ref. [9].

### Box 2. Is gaze a special attentional cue?

Numerous studies have shown that perception of averted gaze triggers an involuntary shift of covert or overt attention towards the gazed-at location (for a review see Ref. [67]). Similar effects are also observed in macaques, indicating a common mechanism mediating reflexive social attention in both species [68]. The gaze-cueing effect has been attributed to the importance of the eyes in social communication and the existence of specialized neural systems for gaze perception, leading to the suggestion that gaze is a 'special' attentional cue that triggers an obligatory social attention reflex. Recent studies have challenged this view, however, by showing that non-biological symbols with 'overlearned' directional meaning, such as direction words (i.e. 'left', 'right') and arrows, also elicit reflexive attention shifts [69].

Inhibition of return (IOR) to a previously attended location is considered as the hallmark of exogenous orienting triggered by salient sensory events. No rapid IOR is observed for gaze [70] or arrow [71] cues (but see Ref. [72] for slowly emerging IOR for gaze cues), supporting the idea that orienting by neither cue type is mediated by the exogenous system. Corroborating evidence comes from a patient with ventromedial prefrontal damage who shows impaired orienting by direction words and gaze, but preserved exogenous orienting [73].

Nevertheless, other research indicates that gaze and arrow cued orienting might operate on different (but not exogenous) attention systems. Nonpredictive arrow but not gaze cues elicit the early direction of attention negativity (EDAN) ERP component associated with voluntary orientation of attention [74], and an fMRI study demonstrated disproportionate engagement of the endogenous orienting system by arrow versus gaze cueing [75]. Furthermore, an investigation [76] of patients with left hemispatial neglect following right parietal damage (in regions contributing to endogenous control of attention [40]) showed cueing effects with gaze but not arrows to both contralesional and ipsilesional sides. It is also more difficult to suppress orienting by gaze than by arrows: it has been shown that gaze [77,78] but not arrow-cueing [77] effects persist when the cues systematically point away from the upcoming target location (although see Ref. [79]). Hence, although these data indicate that automatic attentional shifts by arrow cues are rapid and automatic, they might be mediated by the endogenous attention system. But as no gaze-cueing specific neural effects have been found in neuroimaging studies, future experiments are required to investigate the idea of a 'special' (i.e. neither exogenous nor endogenous) neurocognitive system for gaze-cued orienting.

different gaze directions in human anterior STS [9] (Figure 1b–d). Whether this same region contains identity-invariant representations of different head and body orientations in humans remains to be addressed (but see Ref. [17] for view-specific coding of facial identity using fMRI-adaptation).

## Lesion studies

The aforementioned research indicates a crucial contribution of the STS to coding gaze direction. This is further indicated by work showing that bilateral removal of the STS region in macaques produces impaired perception of gaze direction without significantly affecting facial identity perception [18]. Human lesion studies provide further support for the involvement of the superior temporal areas in the perception of gaze direction. However, the paucity of available data makes it difficult to conclude whether these impairments are gaze-specific. For example, a patient (MJ) with damage to the right superior temporal gyrus (STG) showed impaired gaze discrimination resulting from a rightward bias, that is, a tendency to report left gaze as direct and direct gaze as right [19] (see also Ref. [20] for impaired gaze perception after left STG and inferior parietal lobule damage). MJ also showed a less severe but similar rightward bias in categorising the position of schematic stimuli she did not perceive as gaze, and had recovered from dense hemispatial neglect. Given that right STG damage has an established role in neglect and spatial awareness [21], MJ's impaired gaze perception might reflect a residual spatial impairment that gaze discrimination is particularly sensitive to. This would accord with the suggestion that gaze processing reflects an interaction between sections of STS coding the visual representation of gaze and components of the attention network [22]. The extent of this interaction could be addressed by investigating gaze perception in patients with attentional deficits, such as manifest hemispatial neglect.

Additional work with MJ has shown impaired attentional orienting by gaze but not arrow cues [23]. Although this is supportive of a dissociation between orienting of attention by gaze and symbolic cues (Box 2), it does not exclude the possibility that her gaze discrimination impairment reflects a spatial bias because gaze signals direction via spatial position (i.e. the location of the pupil and iris), whereas arrows do not. Further evidence that orienting of attention by gaze and non-social symbols could rely on partially distinct mechanisms, comes from a study of a split-brain patient (JW) who showed attentional cueing from arrows when the stimuli were presented to either hemisphere [24], but cueing from gaze for right hemisphere presentations only [25]. However, it is possible that the right hemisphere dominance reflects the predominant role of this hemisphere in face and gaze perception. In other words, the hemisphere effect might be attributable to a more fundamental distinction between visual perception of face and non-face cues, rather than attentional orienting from gaze and arrows *per se*.

In summary, although lesion studies support the involvement of the STS in gaze perception, more research is required to determine whether these impairments are gaze-specific. In the absence of extensive lesion work, neuroimaging studies have proved particularly informative. Again, they have focussed on gaze, rather than head or body orientation.

## Human neuroimaging studies

Although comparative work and lesion studies emphasized the role of the STS in social attention, neuroimaging studies in humans have shown that a much more extensive neural network is involved. Moreover, recent work indicates that the STS is not simply involved in the visual analysis of gaze. Although single-cell recordings in monkeys and fMRI-adaptation of gaze perception [9] found that the anterior STS contained cells sensitive to different gaze directions, the majority of human fMRI research has identified the involvement of the posterior 'STS region' (i.e. pSTS and adjacent middle and superior temporal gyri [26]). However, standard group-based comparisons of activation to gaze contact and gaze aversion have shown no consistent pattern of pSTS activation. Some studies have shown increased pSTS involvement for gaze contact [27], some for gaze aversion [28,29] and others equivalent activation to both or no significant difference [30–32]. Given

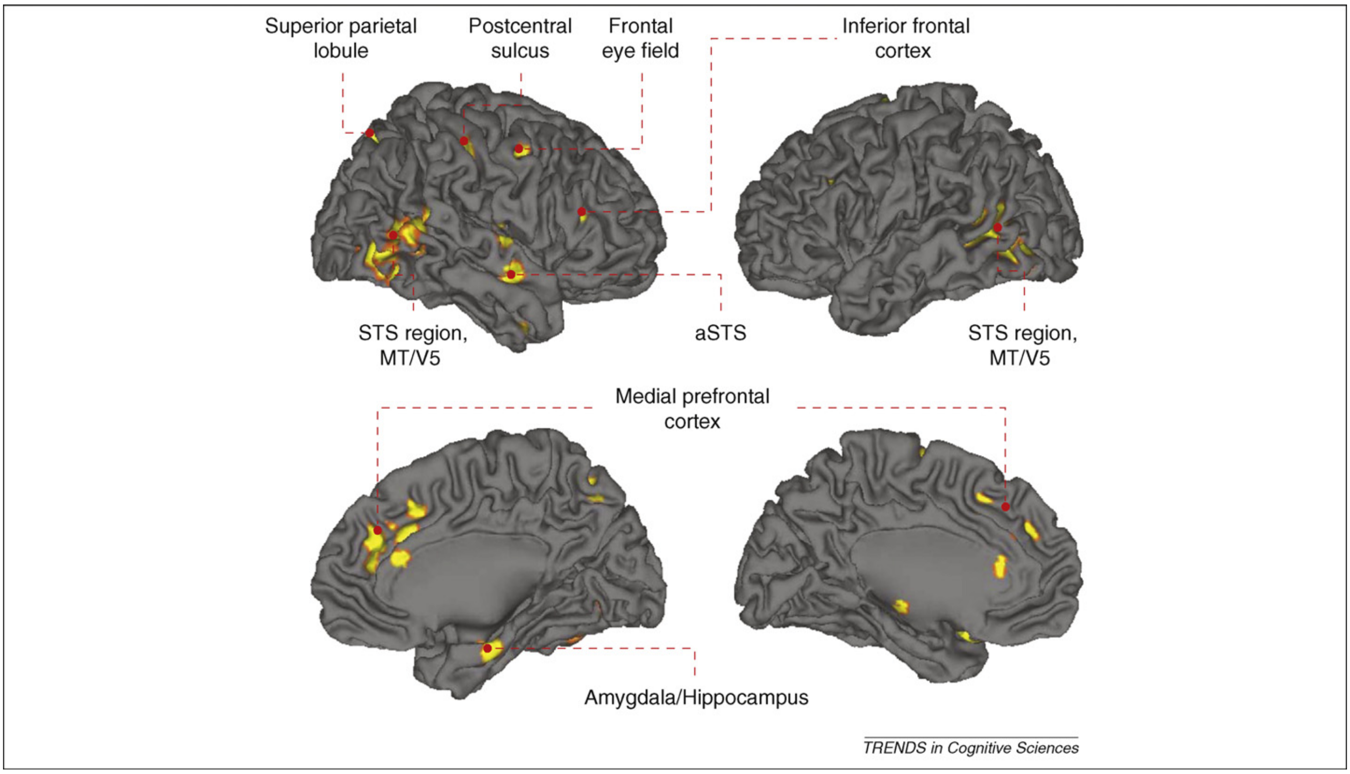


**Figure 2.** Neural topography of eye gaze perception. Eye gaze perception recruits a widespread neural system over occipitotemporal, parietal, medial and lateral prefrontal cortices. The Activation Likelihood Estimation (ALE) method [38,39] quantifies the degree of agreement in 3D-stereotactic coordinates of activation foci across functional imaging studies, and uses significance thresholds to create statistically defensible conclusions (i.e. interstudy consistencies) about the summarized data. The brain regions in this pseudo-statistical parametric image generated with ALE show reliable responses to eye gaze across 178 participants in 16 fMRI and PET studies [9,28–37,75,89–92] ($p < .05$, False Discovery Rate [FDR] corrected). Some studies contribute data from more than one contrast. Contrasts comparing eye gaze to a low-level baseline such as fixation or rest were excluded. Thus, the observed foci do not reflect activation in response to face perception alone.

the lack of consistency, it is possible that the activation is driven at least in part by the behavioural task or context in which the faces are presented, rather than the physical direction of the gaze.

It is also clear that gaze processing extends well-beyond the STS to include the amygdala [30,32], inferior temporal [31], parietal [9,28,31,33,34], medial prefrontal and anterior cingulate cortices [35–37], and other frontal regions [33,34,36,37]. However, these different regions seem to process different aspects of the visual and social properties of gaze. To localize and quantify the reliability of gaze-related brain activations across studies, we summarized the results of human fMRI and positron emission tomography (PET) studies using activation likelihood estimations (ALE) [38,39] (Figure 2).

Consistent with the suggestion that gaze processing involves aspects of the attention network [22], the ALE procedure not only identified the pSTS region but also components of the dorsal attention system (superior parietal lobule [SPL] and frontal eye fields [FEF]) implicated in goal-directed and exogenous shifts in attention [40], supporting the view that humans show an automatic tendency to follow the gaze direction of others (Box 2). Statistically reliable involvement of other regions was also observed. The MT/V5 complex is involved in motion perception and constitutes a crucial initial stage in processing dynamic facial characteristics, such as gaze, facial expressions and facial movements more generally [41]. As already discussed, anterior STS might code individual gaze directions [9], whereas the amygdala/hippocampus might have a particular role in perception of, or monitoring for, gaze contact [30,32,34] and could reflect an emotional response to being looked at (Box 3). The lateral fusiform gyrus is thought to contribute more to facial identity recognition [22], but has been identified in several gaze studies [31,33,34]; its involvement in gaze perception might reflect enhanced attention to faces showing gaze shifts or gaze contact, although this requires further investigation.

The medial prefrontal regions engaged by gaze perception [35,37] have been implicated in theory of mind (ToM) processes (i.e. attributing mental states to others) [42]. These mechanisms could be evoked to infer why a person is gazing at a particular object or to form hypotheses regarding the person's potential goal-directed actions towards the object. For this reason, some have proposed that gaze processing is intrinsically linked with theory of mind [43]. Moreover, the observation that gaze perception and ToM tasks also engage similar regions of pSTS and adjacent temporoparietal junction, prompted the proposal that the pSTS activation to viewing gaze could relate to these sorts of higher-order social processes, rather than visual analysis of gaze alone [35].

This hypothesis is supported by work showing that the same pSTS region is involved in processing other social cues, such as biological motion (including static displays of biological motion stimuli) [26] and 2D 'Heider-Simmel' animations of geometrical shapes moving in a manner

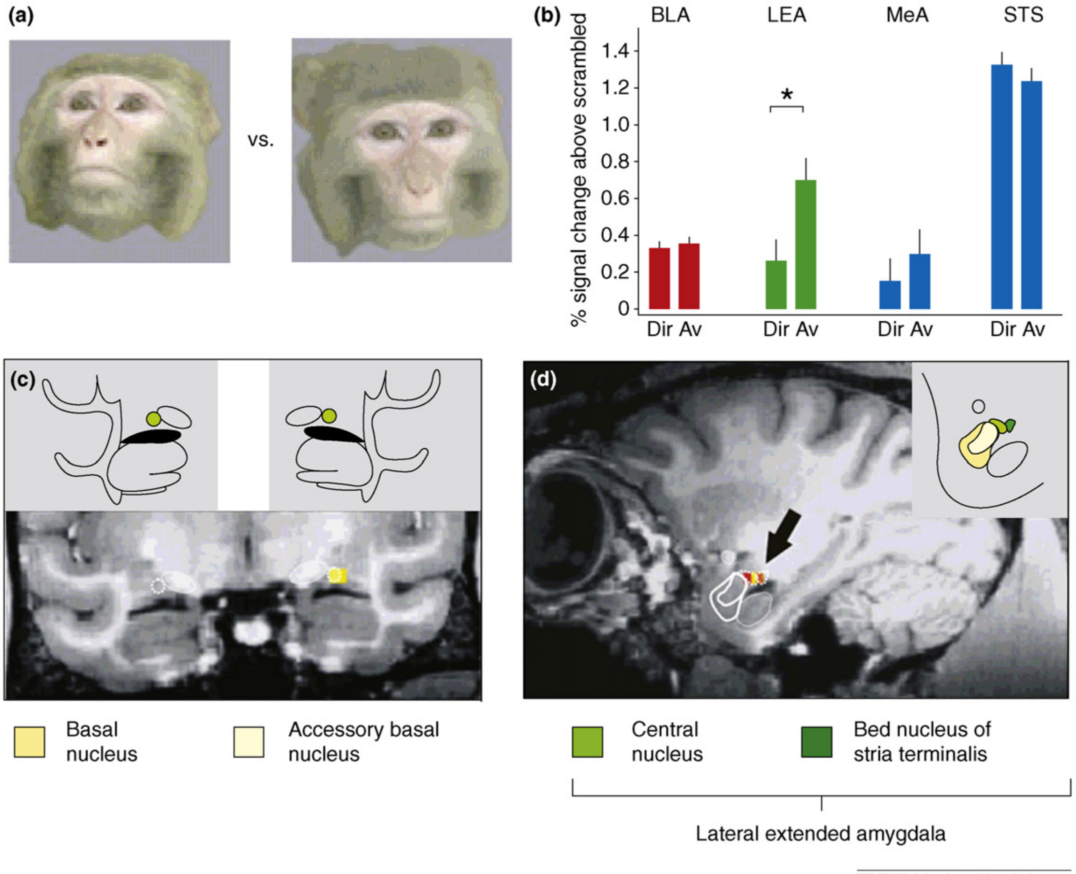
### Box 3. Is the amygdala involved in gaze perception?

The amygdala has been widely implicated in face and facial expression perception. Several studies point to its involvement in gaze perception, but its exact contribution is currently unclear. Single-unit recordings from the medial macaque amygdala have found cells selectively tuned to gaze contact [80]. Similarly, in humans, amygdala activation [32], and functional 'coupling' between the amygdala and face-sensitive fusiform cortex [30], has been shown to increase when viewing (or monitoring for [34]) gaze contact versus gaze aversion.

High-resolution fMRI in awake macaques has shown that specifically the lateral extended amygdala (LEA; including central nucleus and bed nucleus of stria terminalis) is sensitive to social attention direction of other monkeys [81] (Figure I). Because the central nucleus is also involved in vigilance and orienting behaviour, one plausible hypothesis is that it contributes to encoding the behavioural salience or affective arousal evoked by the gaze direction of others. Accordingly, studies in both humans [82] and monkeys [81] have shown that the gaze signal associated with increased amygdala activation (gaze contact for humans, gaze aversion for monkeys) also increases autonomic arousal as indexed by galvanic skin response.

Additional work has shown that gaze can modulate the amygdala response to other facial cues. The amygdala response to facial expressions of fear is greater for direct than averted gaze, and vice versa for angry expressions [83]; although see Ref. [84] for the opposite result for anger. In the case of race perception, other-race faces portraying gaze contact (but not gaze aversion) are perceived as more threatening, and result in increased amygdala activation, than own-race faces [85].

Neuropsychological patient studies also point to the involvement of the amygdala in gaze processing. Both gaze direction perception [86] and attentional orienting by gaze, but not by arrow cues [87], are impaired by amygdala damage. By contrast, patient SM with bilateral amygdala damage shows relatively spared gaze perception [88], although she makes very few spontaneous fixations on the eyes while viewing faces. The latter has been attributed to reduced vigilance for the affective meaning of the eyes. However, whether this can explain gaze processing impairments in other patients with amygdala damage remains to be determined.



TRENDS in Cognitive Sciences

**Figure I.** Encoding social attention direction in the macaque amygdala. Viewing gaze aversion versus gaze contact **(a)** results in an increased response **(b)** in the lateral extended amygdala **(c,d)**. The colour code refers to the anatomical regions of interest shown in insets of (c,d). Abbreviations: BLA, basolateral amygdala; LEA, lateral extended amygdala; MeA, medial amygdala, STS, superior temporal sulcus. Adapted, with permission, from Ref. [81].

interpreted as socially meaningful [44]. All of these signals convey actions but also intentions. Therefore, it is of note that single-cell recordings in the monkey STS have shown that, in addition to cells responding to the gaze, body posture and limb movements of others, a subset of the limb movement cells were modulated by the seen agent's focus of attention [45]. The authors [45] proposed that this combination underlies the detection of intentional actions.

Neuroimaging studies have provided evidence of similar mechanisms in human STS (Figure 3). One study showed that the pSTS is engaged more when subjects view faces gazing away rather than towards the location of an immediately preceding target, violating 'expected intentionality' and perhaps requiring more processing effort [33,46]. A comparable effect has been observed using directed grasping actions in place of gaze shifts [47].

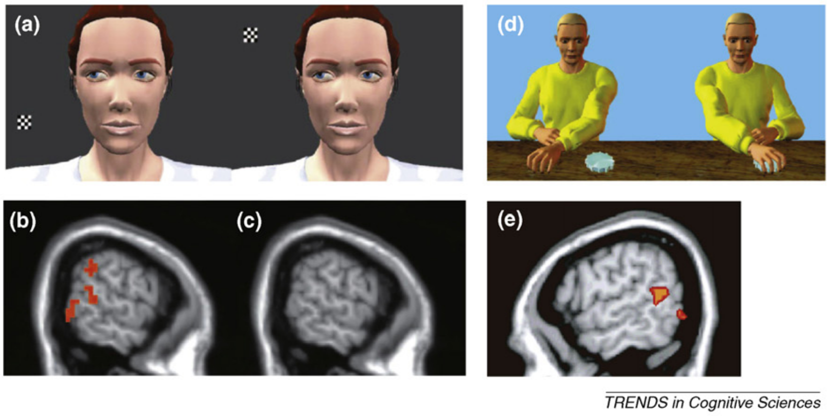


**Figure 3**. The posterior portion of the STS responds to the intentionality of gaze shifts and other actions. **(a,b)** Viewing an animated character looking away rather than towards the location of a checkerboard target results in an increased response in the right pSTS region [49]. This is thought to reflect the violation of an intentionality expectation, potentially resulting in more processing effort. **(c)** This effect is not observed in individuals with ASC [49] who nevertheless show accurate gaze direction judgements [50], indicating a dissociation between perceptual and post-perceptual mechanisms involved in gaze perception. **(d,e)** The same pSTS region also responds to a similar paradigm in which an animated character (whose gaze is held constant) makes a grasping action away from or towards the location of a target object [47], implying that the pSTS might serve a more general function in detecting intentions of human actions. (a–c) Adapted, with permission, from Ref. [49], (d–e) Adapted, with permission, from Ref. [47].

Increased pSTS activation is also found when participants view a person pausing while walking from one location to another [48]. It is particularly interesting that the effect for gaze is absent in individuals with ASC [49] who show preserved gaze perception but impaired interpretation of mental states from gaze [50,51], further underlining the involvement of the pSTS in social cognitive processes. Additional support comes from a study in which participants viewed an animated figure walking towards them and then looking directly at or away from them [27]. Both could be accomplished by a leftwards or rightwards gaze shift, depending on the position of the figure. However, gaze contact (potentially signalling greater intentionality towards the viewer) produced a greater pSTS response, relative to averted gaze. Similarly, an EEG study has shown that viewing dynamic leftward or rightward shifts in gaze direction that establish gaze contact (versus gaze aversion) produced an enhanced N170 component localized to the pSTS [52]. A similar observation was found using magnetoencephalography (MEG), although here the effect was localized to the MT/V5, which lies adjacent to the pSTS [53]. These findings contrast with research showing that viewing static images of direct (i.e. gaze contact) or averted gaze produced no differential ERP amplitudes in adults [54,55]. This could be because static images do not convey a deliberate intention to look at or away from the participant as clearly as a sudden change in gaze direction. Taken together, there is increasing evidence that pSTS region is sensitive to the intentionality conveyed by gaze and other social cues. However, whether this reflects a direct role for this region in processing intentionality, or feedback from other areas with a more established role in mental state attribution, such as the medial prefrontal cortex (mPFC), remains to be established.

## Typical and atypical development of gaze perception

Recent developmental studies have shown that heightened sensitivity to gaze contact is evident at a remarkably early age (see Ref. [56] for a review). Four-day-old infants prefer to look at faces portraying gaze contact as opposed to gaze aversion [57], and at four-months show enhanced occipital midline ERPs (the putative infant equivalent of the face-sensitive N170 component in adults) to gaze contact versus aversion across multiple head orientations [57,58]. By three months, averted gaze has also gained some meaning, as shown by preferential eye movements towards the direction of adults' gaze [59]. Moreover, by the age of five the enhanced ERP response to gaze contact is absent, and remains absent in adulthood [54]. This has led to the suggestion [54] that the social relevance of averted gaze increases with development, resulting in equivalent ERPs to direct and averted gaze. However, the social relevance of gaze might depend on the mode of presentation (i.e. static versus dynamic stimuli) because, as already discussed, increased sensitivity to gaze contact is found in adults using socially salient dynamic gaze shifts [52,53].

Further developmental work has indicated that learning the pairing between another's gaze direction and a potentially rewarding event at the gazed-at location might reinforce the use of gaze as a social cue, and promote development of 'social' gaze-following behaviour (see Ref. [51]). By six-months of age, infants seem to understand the social communicative value of gaze, as illustrated by research showing that gaze following in infants requires that the gaze shift is preceded by an ostensive signal, such as gaze contact or vocal communication [60].

The early sensitivity to gaze cues in neonates is in sharp contrast to the developmental deficits in certain aspects of gaze processing observed in individuals with ASC. Although individuals with ASC show relatively unimpaired discrimination of the gaze direction of others, they demonstrate an impaired ability to infer the mental states of others (e.g. intentions) from their gaze [50,51]. Such 'mind blindness' generalizes to numerous social cues and has been argued to explain behavioural and social deficits in ASC [43]. Of interest, five-year-olds with ASC show strikingly similar ERPs as younger infants when passively viewing gaze contact versus gaze aversion [54]. A likely explanation for this is that the individuals with ASC have not learned to associate gaze with social intentions (see also Ref. [49]), and thus do not perceive averted gaze as a salient cue. Nevertheless, individuals with ASC show some rudimentary gaze following functions, indicating that mental state attribution is not always required for gaze following. Most studies show that individuals with ASC manifest reflexive orienting to nonpredictive gaze direction in a cueing task, although it is possible that unlike typically developing individuals, they might not process the eyes via gaze-specific mechanisms (for a review, see Ref. [51]). In line with this, gaze-selective ERPs in typically developing children are lateralized to the right, whereas a similar asymmetry is not observed in children with ASC [61]. Thus, the lack of ability to infer the social meaning of gaze could explain why the covert gaze following reflex does not generalize to joint attention in social encounters [62].

Together these data indicate that, although elementary gaze detection skills could be innate, interpreting the social function of gaze develops during the first year of life. The early abnormal sensitivity to social meaning of gaze in ASC might lead to subsequent difficulties in learning to interpret others' intentions from social cues [49,50] and engaging in extended joint attention during social interaction [62], which could ultimately contribute to the development of 'mind blindness'. In future ERP studies, it could be interesting to track the longitudinal time course of atypical gaze processing in infants at risk of developing ASC; indeed this could provide a potential reliable early marker of ASC.

## Conclusions

In accord with single-cell recording research in macaques [2], recent adaptation experiments show that different gaze, body and head directions are coded by a limited number of separate channels [4,10], with initial fMRI-adaptation work pointing to the involvement of anterior STS in coding different gaze directions [9]. Human neuroimaging studies more generally show that perception of social attention recruits a widely distributed network, involving temporal areas implicated in face perception (i.e. fusiform gyrus and STS), frontoparietal attention regions (i.e. SPL, FEF) and areas implicated in emotion and social cognition (i.e. amygdala and mPFC). Respectively, these regions are thought to underlie visual analysis of social attention direction, imitative attention shifts, emotional reactions and mental state attribution. Of particular interest, recent neuroimaging research demonstrates that the pSTS region is sensitive to the intentionality conveyed by gaze and other social signals, indicating a potential dissociation with the anterior STS coding different gaze directions. However, additional research will be required to validate this distinction and whether the pSTS is directly involved in this form of mental state attribution, or is modulated by other areas with a more established role in theory of mind.

Although research in gaze processing is beginning to outline the functional and neural bases of social attention, much work (Box 4) is needed to establish the time course, interactions and development of the different components of this system. Consequently, we feel that a 'box-and-arrow' model of social attention or gaze processing would be premature and potentially misleading at this time. Future studies should also focus more on other social attention cues, such as head and body orientation and pointing gestures, to assess whether the network identified in Figure 2 reflects the neural substrates of gaze or social attention in general.

### Box 4. Outstanding questions

- Do the brain regions involved in gaze perception (Figure 2 in main text) constitute a functional network? Effective connectivity modelling using fMRI could address how posterior temporal areas (i.e. pSTS and fusiform gyrus) interact with other areas implicated in gaze processing.
- As lesion studies of the brain regions involved in gaze perception are limited, it would be informative to target the regions shown in Figure 2 (in main text) with transcranial magnetic stimulation (TMS) to validate their roles in social attention perception.
- Behavioural studies have shown that individual differences in attentional control [79] and autistic-like traits [78] influence processing of social attention cues. Determining how such individual differences affect the regional functioning and interconnectivity of the brain systems implicated in social attention perception would provide important insight into the neural basis of social cognitive disorders.
- Much of the work on social attention perception has been conducted using static images or schematic stimuli, but given the important role of the STS in integrating form and motion, experiments of social attention perception using dynamic stimuli are needed to establish the role of this region in processing stimuli that are more naturalistic.

## Acknowledgements

This work was supported by Academy of Finland grant #119088 to L.N. and MRC project code U.1055.02.001.0001.01 to A.J.C. We thank Michael Ewbank, Teresa Farroni, Tobias Grossmann, Jukka Hyönä and Professor David Perrett for their helpful comments on earlier versions of this paper.

## References

1 Emery, N.J. (2000) The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci. Biobehav. Rev.* 24, 581–604

2 Perrett, D.I. *et al.* (1992) Organization and functions of cells responsive to faces in the temporal cortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci. B335* 23–30

3 Jenkins, R. *et al.* (2006) I thought you were looking at me: direction-specific aftereffects in gaze perception. *Psychol. Sci.* 17, 506–513

4 Lawson, R.P. *et al.* About turn: the visual representation of human body orientation revealed by adaptation. *Psychol. Sci.* (in press)

5 Fang, F. *et al.* (2007) Transfer of the face viewpoint aftereffect from adaptation to different and inverted faces. *J. Vis.* 7, 1–9

6 Webster, M.A. (1996) Human colour perception and its adaptation. *Comput. Neural Syst.* 7, 587–634

7 Clifford, C.W.G. (2002) Adaptation-induced plasticity in perception: motion parallels orientation. *Trends Cogn. Sci.* 6, 136–143

8 Rhodes, G. *et al.* (2005) Adaptation and face perception: how aftereffects implicate norm-based coding of faces. In *Fitting the Mind to the World* (Clifford, C.W.G. and Rhodes, G., eds), pp. 213–240, Oxford University Press

9 Calder, A.J. *et al.* (2007) Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Curr. Biol.* 17, 20–25

10 Calder, A.J. *et al.* (2008) Visual representation of eye gaze is coded by a nonopponent multichannel system. *J. Exp. Psychol. Gen.* 137, 244–261

11 Leopold, D.A. *et al.* (2001) Prototype-referenced shape encoding revealed by high-level after effects. *Nat. Neurosci.* 4, 89–94

12 Schweinberger, S.R. *et al.* (2007) Are you looking at me? Neural correlates of gaze adaptation. *Neuroreport* 18, 693–696

13 Jacques, C. *et al.* (2007) The time course of the inversion effect during individual face discrimination. *J. Vision* 7, 1–9

14 Bentin, S. *et al.* (1996) Electrophysiological studies of face perception in humans. *J. Cogn. Neurosci.* 8, 551–565

15 Wachsmuth, E. *et al.* (1994) Recognition of objects and their component parts: responses of single units in the temporal cortex of the macaque. *Cereb. Cortex* 4, 509–522

16 Grill-Spector, K. *et al.* (2006) Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* 10, 14–23

17 Fang, F. *et al.* (2007) Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. *Cereb. Cortex* 17, 1402–1411

18 Heywood, C.A. and Cowey, A. (1992) The role of the 'face-cell' area in the discrimination and recognition of faces by monkeys. *Philos. Trans. R. Soc. Lond. B Biol. Sci. B335* 31–38

19 Akiyama, T. *et al.* (2006) A deficit in discriminating gaze direction in a case with right superior temporal gyrus lesion. *Neuropsychologia* 44, 161–170

20 Samson, D. *et al.* (2004) Left temporoparietal junction is necessary for representing someone else's belief. *Nat. Neurosci.* 7, 499–500

21 Karnath, H-O. *et al.* (2001) Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature* 411, 950–953

22 Haxby, J.V. *et al.* (2000) The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233

23 Akiyama, T. *et al.* (2006) Gaze but not arrows: a dissociative impairment after right superior temporal gyrus damage. *Neuropsychologia* 44, 1804–1810

24 Ristic, J. *et al.* (2002) Are eyes special? It depends on how you look at it. *Psychon. Bull. Rev.* 9, 507–513

25 Kingstone, A. *et al.* (2000) Reflexive joint attention depends on lateralized cortical connections. *Psychol. Sci.* 11, 159–166

26 Allison, T. *et al.* (2000) Social perception from visual cues: role of the STS region. *Trends Cogn. Sci.* 4, 267–278

27 Pelphrey, K.A. *et al.* (2004) When strangers pass: processing of mutual and averted gaze in the superior temporal sulcus. *Psychol. Sci.* 15, 598–603

28 Hoffman, E.A. and Haxby, J.V. (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat. Neurosci.* 3, 80–84

29 Engell, A.D. and Haxby, J.V. (2007) Facial expression and gaze-direction in human superior temporal sulcus. *Neuropsychologia* 45, 3234–3241

30 George, N. *et al.* (2001) Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *Neuroimage* 13, 1102–1112

31 Wicker, B. *et al.* (1998) Brain regions involved in the perception of gaze: a PET study. *Neuroimage* 8, 221–227

32 Kawashima, R. *et al.* (1999) The human amygdala plays an important role in gaze monitoring – a PET study. *Brain* 122, 779–783

33 Mosconi, M.W. *et al.* (2005) Taking an 'intentional stance' on eye-gaze shifts: a functional neuroimaging study of social perception in children. *Neuroimage* 27, 247–252

34 Hooker, C.I. *et al.* (2003) Brain networks for analyzing eye gaze. *Brain Res. Cogn. Brain Res.* 17, 406–418

35 Calder, A.J. *et al.* (2002) Reading the mind from eye gaze. *Neuropsychologia* 40, 1129–1138

36 Bristow, D. *et al.* (2007) Social interaction modifies neural response to gaze shifts. *Soc. Cogn. Affect. Neurosci.* 2, 52–61

37 Williams, J.H.G. *et al.* (2005) An fMRI study of joint attention experience. *Neuroimage* 25, 133–140

38 Turkeltaub, P.E. *et al.* (2002) Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. *Neuroimage* 16, 765–780

39 Chein, J.M. *et al.* (2002) Functional heterogeneity within Broca's area during verbal working memory. *Physiol. Behav.* 77, 635–639

40 Corbetta, M. *et al.* (2008) The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324

41 O'Toole, A.J. *et al.* (2002) Recognizing moving faces: a psychological and neural synthesis. *Trends Cogn. Sci.* 6, 261–266

42 Gallagher, H.L. and Frith, C.D. (2003) Functional imaging of 'theory of mind'. *Trends Cogn. Sci.* 7, 77–83

43 Baron-Cohen, S. (1995) *Mindblindness: An Essay on Autism and Theory of Mind.* MIT press

44 Castelli, F. *et al.* (2000) Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage* 12, 314–325

45 Jellema, T. *et al.* (2000) Neural representation for the perception of intentionality of actions. *Brain Cogn.* 44, 280–302

46 Pelphrey, K.A. *et al.* (2003) Brain activation by perception of gaze shifts: the influence of context. *Neuropsychologia* 41, 156–170

47 Pelphrey, K.A. *et al.* (2004) Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *J. Cogn. Neurosci.* 16, 1706–1716

48 Saxe, R. *et al.* (2004) A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia* 42, 1435–1446

49 Pelphrey, K.A. *et al.* (2005) Neural basis of eye gaze processing deficits in autism. *Brain* 128, 1038–1048

50 Baron-Cohen, S. *et al.* (1995) Are children with autism blind to the mentalistic significance of the eyes? *Dev. Psychol.* 12, 379–398

51 Nation, K. and Penny, S. (2008) Sensitivity to eye gaze in autism: is it normal? Is it automatic? Is it social?. *Dev. Psychopathol.* 20, 79–97

52 Conty, L. *et al.* (2007) When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. *Neuropsychologia* 45, 3024–3037

53 Watanabe, S. *et al.* (2006) Human MT/V5 activity on viewing eye gaze changes in others: a magnetoencephalographic study. *Brain Res.* 1092, 152–160

54 Grice, S.J. *et al.* (2005) Neural correlates of eye-gaze detection in young children with autism. *Cortex* 41, 342–353

55 Taylor, M.J. *et al.* (2001) Direction of gaze effects on early face processing: eyes-only versus full faces. *Brain Res. Cogn. Brain Res.* 10, 333–340

56 Senju, A. and Johnson, M.H. (2009) The eye contact effect: mechanism and development. *Trends Cogn. Sci.* 13, 127–134

57 Farroni, T. *et al.* (2002) Eye contact detection in humans from birth. *Proc. Natl. Acad. Sci. U. S. A.* 99, 9602–9605

58 Farroni, T. *et al.* (2004) Mechanisms of eye gaze perception during infancy. *J. Cogn. Neurosci.* 16, 1320–1326

59 Hood, B.M. *et al.* (1998) Adult's eyes trigger shifts of visual attention in human infants. *Psychol. Sci.* 9, 131–134

60 Senju, A. and Csibra, G. (2008) Gaze following in human infants depends on communicative signals. *Curr. Biol.* 18, 668–671

61 Senju, A. *et al.* (2005) Deviant gaze processing in children with autism: an ERP study. *Neuropsychologia* 43, 1297–1306

62 Dawson, G. *et al.* (2004) Early Social attention impairments in autism: social orienting, joint attention, and attention to distress. *Dev. Psychol* 40, 271–283

63 Perrett, D.I. *et al.* (1985) Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proc. R. Soc. Lond. B. Biol. Sci.* B223, 293–317

64 De Souza, W.C. *et al.* (2005) Differential characteristics of face neuron responses within the anterior superior temporal sulcus of macaques. *J. Neurophysiol.* 94, 1252–1266

65 Langton, S.R.H. (2000) The mutual influence of gaze and head orientation in the analysis of social attention direction. *Q. J. Exp. Psychol. A* 53, 825–845

66 Ricciardelli, P. and Driver, J. (2008) Effects of head orientation on gaze perception: how positive congruency effects can be reversed. *Q. J. Exp. Psychol.* 61, 491–504

67 Frischen, A. *et al.* (2007) Gaze cueing of attention: visual attention, social cognition, and individual differences. *Psychol. Bull.* 133, 694–724

68 Deaner, R.O. and Platt, M.L. (2003) Reflexive social attention in monkeys and humans. *Curr. Biol.* 13, 1609–1613

69 Hommel, B. *et al.* (2001) Symbolic control of visual attention. *Psychol. Sci.* 12, 360–365

70 Friesen, C.K. and Kingstone, A. (1998) The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychon. Bull. Rev.* 5, 490–495

71 Muller, H.J. and Rabbitt, P.M.A. (1989) Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 315–330

72 Frischen, A. and Tipper, S.P. (2004) Orienting attention via observed gaze shift evokes longer term inhibitory effects: implications for social interactions, attention, and memory. *J. Exp. Psychol. Gen.* 133, 516–533

73 Vecera, S.P. and Rizzo, M. (2004) What are you looking at?: impaired 'social attention' following frontal-lobe damage. *Neuropsychologia* 42, 1657–1665

74 Hietanen, J.K. *et al.* (2008) Visuospatial attention shifts by gaze and arrow cues: an ERP study. *Brain Res.* 1215, 123–136
75 Hietanen, J.K. *et al.* (2006) Automatic attention orienting by social and symbolic cues activates different neural networks: an fMRI study. *Neuroimage* 33, 406–413
76 Vuilleumier, P. (2002) Perceived gaze direction in faces and spatial attention: a study in patients with parietal damage and unilateral neglect. *Neuropsychologia* 40, 1013–1026
77 Friesen, C.K. *et al.* (2004) Attentional effects of counterpredictive gaze and arrow cues. *J. Exp. Psychol. Hum. Percept. Perform.* 30, 319–329
78 Bayliss, A.P. and Tipper, S.P. (2006) Predictive gaze cues and personality judgments: should eye trust you? *Psychol. Sci.* 17, 514–520
79 Tipples, J. (2008) Orienting to counterpredictive gaze and arrow cues. *Percept. Psychophys.* 70, 77–87
80 Brothers, L. and Ring, B. (1993) Mesial temporal neurons in the macaque monkey with responses selective for aspects of social-stimuli. *Behav. Brain Res.* 57, 53–61
81 Hoffman, K.L. *et al.* (2007) Facial-expression and gaze-selective responses in the monkey amygdala. *Curr. Biol.* 17, 766–772
82 Hietanen, J.K. *et al.* (2008) Seeing direct and averted gaze activates the approach-avoidance motivational brain systems. *Neuropsychologia* 46, 2423–2430
83 Adams, R.B. *et al.* (2003) Effects of gaze on amygdala sensitivity to anger and fear faces. *Science* 300, 1536
84 Sato, W. *et al.* (2004) The amygdala processes the emotional significance of facial expressions: an fMRI investigation using the interaction between expression and face direction. *Neuroimage* 22, 1006–1013
85 Richeson, J.A. *et al.* (2008) Eye-gaze direction modulates race-related amygdala activity. *Group Process. Intergroup Relat.* 11, 233–246
86 Young, A.W. *et al.* (1995) Face processing impairments after amygdalotomy. *Brain* 118, 15–24
87 Akiyama, T. *et al.* (2007) Unilateral amygdala lesions hamper attentional orienting triggered by gaze direction. *Cereb. Cortex* 17, 2593–2600
88 Adolphs, R. *et al.* (1998) The human amygdala in social judgment. *Nature* 393, 470–474
89 Kingstone, A. *et al.* (2004) The eyes have it!: an fMRI investigation. *Brain Cogn.* 55, 269–271
90 Kato, C. *et al.* (2001) Activation during endogenous orienting of visual attention using symbolic pointers in the human parietal and frontal cortices: a functional magnetic resonance imaging study. *Neurosci. Lett.* 314, 5–8
91 Materna, S. *et al.* (2008) Dissociable roles of the superior temporal sulcus and the intraparietal sulcus in joint attention: a functional magnetic resonance imaging study. *J. Cogn. Neurosci.* 20, 108–119
92 Puce, A. *et al.* (1998) Temporal cortex activation in humans viewing eye and mouth movements. *J. Neurosci.* 18, 2188–2199