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Eye to eye, face to face and brain to brain: novel approaches to study the behavioral dynamics and neural mechanisms of social interactions

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The gaze of others fascinates us from birth onwards. Traditionally, experimental approaches to study the effects of gaze have focused on how human observers respond to gaze cues and how attention, perception and action control is influenced by them. In recent years, the investigation of gaze behavior has moved toward the inclusion of more ecologically valid conditions, in which gaze signals are exchanged as part of an ongoing reciprocal social interaction. Such an 'interactive turn' is beginning to yield new insights into the behavioral dynamics and neural mechanisms of gaze behavior as they unfold in real life.

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The special case of gaze

Successful interpersonal communication depends to a large extent upon the exchange of nonverbal information. The face is known to be of particular importance in this respect and whenever we look at a face the eyes are the primary and most consistent target of our visual attention [1]. Despite later-developing skills to navigate the social world, gaze remains a crucial cue system for our understanding of others and serves a variety of social-cognitive functions [2]. It plays a significant role in the regulation of interpersonal distance and influences our perception and evaluation of a potential or actual interactor [3,4]. Here, the unique morphology of the human eye [5] facilitates the detection of gaze direction in other individuals [6] thereby providing important cues about the attentional (and other mental) states of others. Fittingly, social gaze has, therefore, been termed a 'window into social cognition' [7]. Consequently, the behavioral functions and neural mechanisms of gaze behavior are of great interest to a wide range of disciplines encompassing social psychology, linguistics, human–computer interaction, developmental and evolutionary psychology and social neuroscience.

Until recently, however, gaze behavior in social contexts has been studied by using comparably static and non-interactive laboratory experiments, which investigate how a human observer responds to being exposed to gaze cues, while her responses are not fed back into the cue system which has elicited them. Such research has shown that a variety of face-like and gaze stimuli can be effective in modulating visual attention in human observers and that factors, which pertain to both the characteristics of the face and of the human observer can influence such effects. Furthermore, research indicates that people do not only use gaze to acquire information about others, but also use it to signal back to them [8,9]. Finally, recent developments of the study of social gaze and related empirical findings emphasize that certain gaze-related phenomena are interactively constituted, that is depend upon participation in social interaction rather than observation, and may differ significantly depending upon the role one adopts in an interaction, that is the one of being a leader or follower in the social exchange [10].

Core processes of social gaze

Mutual gaze

Being looked at has profound effects on a human observer [11,12]. In fact, the ability to discriminate between direct and averted gaze exists across different species and may have evolved, because direct gaze can signal that a predator is attending [6]. Many animals, therefore, respond to direct gaze with displays of fear, aggression or submission [13]. In humans, initial eye contact (in particular when combined with the so-called 'eye-brow flash' [14]) is transculturally recognized as an approach signal and humans may expect that gaze is directed toward them [15••], whereas prolonged eye contact can be perceived as a threat signal [16]. But any gaze-based social interaction really only starts with two individuals looking at each other, a situation often referred to as *mutual* gaze. Mutual gaze illustrates a key feature of social gaze, namely that perception and action are coupled in single acts of looking [17]. Numerous studies have found that mutual gaze has a profound impact on cognition and emotion across the life-span, a phenomenon referred to as the 'eye contact effect' [18]. For example, it has been shown that faces displaying direct gaze are responded to faster [19] and memorized better than faces with averted gaze [20]. Direct gaze also speeds up the identification of faces and facial expressions [21]), has a positive effect on our judgment of the attractiveness and likeability of others [22] and the likeability of objects associated with them [23]. Most importantly, an initial look toward someone increases the probability of an ensuing conversation and decreases the incidence of no talking [24]. A recently proposed model [18] suggests that on the neural level the 'eye contact effect' is brought about by a subcortical route via the amygdala and low-level visual areas including the superior colliculus and the pulvinar. This subcortical mechanism is though to modulate activity in brain areas involved in the detection of gaze direction, such as the superior temporal sulcus (STS), as well as areas relevant for higher-order social cognition, such as the medial prefrontal cortex (mPFC). Recent evidence has shown that, indeed, the amygdala is relevant for early processing (170 ms) of emotional content of socio-communicative cues, whereas gaze direction cues were combined at approximately 190 ms in the parietal and motor cortices, thereby possibly facilitating the preparation of an adaptive response to another person's intentional state [25].

Gaze-cueing & gaze-following

To look where others are looking can be useful at times. Indeed, from an evolutionary perspective following the gaze of others is considered a prerequisite for certain types of transgenerational learning processes and also non-human primates have been shown to successfully follow the gaze of conspecifics and experimenters [26]. Similarly, neurotypically developing human infants show evidence for gaze-following of care-givers from early ages onwards [27–29]. In well established gaze-cueing/-following paradigms, the influence of a gaze cue on attentional processing is examined and participants are often asked to respond to a set of stimuli that vary in what social characteristics they contain (picture of a real face as compared to a virtual agent or robot or a drawing [30–32]). In a typical study, a face stimulus is presented usually shown with direct gaze (or eyes closed), which is followed by averted gaze to the left or right. Subsequently, a target object is shown at one of the two peripheral locations on the screen, which either coincides with the direction of the gaze shift or not and participants reactions times for responding to the target object is measured. Consistent results demonstrate faster reaction times when target objects appear at locations that are spatially congruent with the direction of the gaze shift as compared to locations that are spatially incongruent with the direction of the gaze shift [2]. Taken together, gaze-cueing studies, therefore, provide evidence that using relatively static gaze stimuli can affect human observers' visual attention in such a way that they shift or align their attention with that of others. Interestingly, other research shows that shifts in attention do not only depend upon perceiving the stimulus as social, but are also influenced by the type of social information conveyed as well as the status of the human observer. For instance, more masculine looking faces and faces that resemble the human observer lead to greater gaze cueing effects [34,35]. Differences in group membership, social and hormonal status, but also autistic and socially anxious traits and likelihood of mental state attribution have been shown to modulate gaze cueing effects [36–44]. Lastly, it was also shown that gaze cueing effects are enhanced after observing eye contact, which could be taken to suggest that these effects can be modulated in the context of a social interaction [45].

Apart from evidence that demonstrates that social gaze can cause shifts in attention, there are also findings, which indicate that gaze cues can change the perception of objects located in the direction of gaze [46,47,48•] and how these objects will be manipulated by an observer [49,50]. These findings suggest differences in the neural networks subserving action control driven by social cues as compared with nonsocial cues. Indeed, an fMRI study [51] provided evidence that executing simple manual actions (i.e. button presses) in a — albeit minimal — gaze-based social context as compared to performing them in a non-social context significantly changes the neural correlates of action control: whereas a fronto-parietal network and the locus coeruleus was differentially recruited when participants had to generate spatially incongruent responses, performing such actions in a social context was subserved by activity change in subcortical structures, anterior cingulate and inferior frontal cortex. Furthermore, difficulties in disengaging from the social (but not non-social) stimuli were correlated with signal change in reward-related neurocircuitry suggesting that interindividual differences exist in social responsiveness, which impact action control in social settings. Consistent with these findings that demonstrate how a gaze-based social context influences action control, an elegant set of recent studies demonstrated that gaze can enhance mimicry of intransitive hand movements and that this is related to a gaze-based modulation of connectivity strength between different components of the 'social' brain, namely mPFC and STS [52,53].

Gaze in interaction: novel methods and findings

The paradigms described above have been extremely helpful in unraveling some effects of gaze cues on attentional processing and action control. One important limitation of this line of research, however, consists in not being able to capture the interactive nature of gaze-based exchanges in the real-world [54,55]. In some sense this research remains restricted to focusing on social perception 'from an observer's point of view', where responses produced by the observer are not fed back to the social world that has elicited them. Recent developments both in experimental psychology, philosophy and neuroscience emphasize the role of active engagement with others in interaction (social cognition 'from an interactor's point of view') as an important route to understanding them [56]. Consequently, the reciprocity of social interactions has received re-newed attention in recent years. Here, research into gaze behavior has been at the forefront of what could be described as an 'interactive turn' in social cognition research. In the context of an ecologically valid, real-time social interaction, participants of an interaction stand in reciprocal relations to each other, which means that they can mutually affect each other, corregulate their behavior and take turns during the social encounter [57]. As a consequence, participants of a reciprocal interaction may hold different roles (of leader or follower) during an interaction and actions may be performed at one point to initiate social contact, while a similar (or even identical) action could later be used again to respond, which highlights the importance of the historicity of an interaction that results from taking the reciprocity of social interaction seriously.

In order to achieve greater ecological validity in gaze research different approaches have been implemented: one approach includes the investigation of the allocation of visual attention in real life situations. Here, it has been found that visual attention changes in situations with a potential for social interactions compared to the 'isolation paradigms' often used in previous laboratory studies [58]. In one such study participants were asked to walk over a university campus to buy coffee. While doing so a head-mounted camera recorded what they saw from their own first-person perspective. These recordings were later played back to other participants, whose eye-movements were measured while looking on screen. When comparing the eyetracking data from both groups of participants, differences were found between those participants who were watching the videos as compared to those participants who had themselves been in the real-life situation [59]. Similarly, another study found that when being interviewed, interviewees look more to the face and less to the background in a real-life condition, where the interviewer is physically present as compared to a video condition where the interviewer was depicted in a video-clip [60].

Another approach has been to use gaze-contingent stimuli in conjunction with anthropomorphic virtual characters in order to create interactive and socially responsive stimuli [61]. Such a setup, thereby, allows participants to experience their own eye-movements to have an effect on the gaze behavior of another agent. Also, this setup allows us to investigate phenomena whose emergence necessarily depends upon social interaction and its inherent reciprocity. This was demonstrated in an fMRI study [10], which investigated the neural correlates of joint attention, that is, attending to something together with someone and being aware that 'we both' are attending. Importantly, joint attention can occur either as a result of following someone else's gaze toward an object or as a result of directing someone else's gaze toward the object. Results demonstrate differences in the neural correlates of joint attention depending upon it being self-initiated or other-initiated: directing someone else's gaze toward an object oneself activated the ventral striatum (VS), a part of the functional neuroanatomy of reward processing, and the degree of activity change in this region correlated with ratings of subjective experience, which indicated that participants enjoyed looking at objects more 'together with' the virtual other. In a follow-up study, gaze-responsive virtual characters were used to tease apart whether joint attention is experienced as pleasant and motivating, because it constitutes a form of cooperative behavior that relies on shared intentions or because it is an activity that is performed for the sake of mutual enjoyment [62]. During the task, participants were asked to assess whether a virtual agent was either controlled by another human or by a computer, while, in fact, the agent was always controlled by a computer. In a between-subject design, the available information about the alleged other player was varied such that one group of participants was led to believe that the other was helping to solve this task whereas the other group thought that the other player was naïve to their task. On the behavioral level, this difference in instructions resulted in marked differences in the evaluation of the agent's gaze behavior. On the neural level it was shown that even in the absence of a shared goal a gaze-based interaction leads to a differential recruitment of reward-related brain regions.

Finally, studies have begun to tackle the challenging task of investigating gaze behavior and coordination across multiple persons: In one study participants' eye-movements were recorded while they spoke about a TV show and were looking at an array of images of the cast members. These monologs were then played to other listeners who looked at the same images. Analyses of gaze recurrence found that approximately 2 s after a speaker looked at an image, the listener was most likely to be looking at it. Speakers and listeners were more likely than chance to look at the same picture within a window of 6 s [63]. Another study showed that two persons also coordinate their attention when synchronously engaging in interactive dialog [64]: In this study participants were seated in separate rooms, looked at the same images on screen and talked over the phone. Both their shared background knowledge and the visual context as well as beliefs about what was shared influenced gaze coordination, which demonstrates that visual attention becomes more closely coordinated during social interaction. In another study, the interaction between gaze and language was investigated using a real-world paradigm, in which participants were asked to build abstract structures from building blocks together with another person. Here, it was shown that gaze cues can increase performance under conditions of ambiguous explicit instructions [65].

Recently, two other methods have been implemented that target the investigation of gaze behavior by means of different implementations of virtual reality: 'proxemic imaging' constitutes a method of creating frequency images of interpersonal space by combining motion capture data of interpersonal distance and gaze to provide an objective analysis of real-time social interactions between human participants and avatars [66]. In a first study that made use of this technology in combination with an economic game with fair and unfair players, it was demonstrated that participants kept the fair player in closer physical proximity. However, participants who chose to punish unfair players later were more likely to stand in front of those players. These patterns, therefore, illustrate that fairness violations have a strong impact on nonverbal behavior and that these subtle behavioral differences can be captured by motion capturing techniques and predict overt norm-enforcing behavior. Another approach has been to combine eyetracking measures of two participants with virtual reality-based renditions of those participants [67]: In this setup, participants can work on tasks cooperatively or individually while being exposed to real-time displays of the respective other participant's gaze behavior as shown by a virtual character. Using such a virtual reality-based interface has the advantage of being able to control the bandwidth and to systematically manipulate the exchange of gaze cues between the two participants. Apart from being able to relate individual task performance and subjective confidence to measures of interpersonal gaze coupling, measures of interpersonal coupling could be also be used to interrogate psychophysiological measures or brain data obtained from one or both brains.

Interestingly, a two-person fMRI setup using live video feeds (rather than virtual reality) to investigate gaze exchanges has already been introduced [68]. In this setup, two interconnected fMRI scanners were equipped with eyetracking systems and cameras to capture both participants' eye regions. The resulting video images were transferred in real time to the upper half of the screen of the other participant. The lower half was used for stimulus presentation to both participants, which consisted of targets that were presented on the left and the right side of the screen. In a 2×2 design, the participants' task was to shift their gaze either according to a gaze cue by the other participant or in response to a color change by one of the targets. In so-called concordant blocks, they had to look in the same direction, whereas discordant blocks required a gaze shift to the opposite target. A condition in which participants were instructed to engage in mutual gaze in the absence of the targets served as a high-level baseline. Results demonstrated that dorsal MPFC and right inferior frontal gyrus (rIFG) showed increased activity during all gaze-cued (as compared to target-cued) trials. Furthermore between-subject brain synchronization was analyzed during the baseline condition, in which participants engaged in mutual gaze. This analysis indicated the rIFG as a locus of neural synchronization and was interpreted by the authors as a 'readiness potential' for subsequent gaze-based interactions.

Conclusions

The present review illustrates that an important line of research exists in the behavioral and brain sciences, which has demonstrated that a variety of face-like and gaze stimuli can be effective in modulating visual attention and action control in human observers. Furthermore, this research indicates that people do not only use gaze cues to acquire information about others from an observational stance, but also use it to directly engage in reciprocal exchanges with them. Such gaze-based exchanges may give rise to interactively constituted phenomena, whose behavioral correlates and neural mechanisms can be explored thanks to the development of innovative experimental paradigms and tools of analysis. While this work is still in its infancy, it has already yielded important insights into the behavioral dynamics and neural mechanisms of real-time social interactions. Such work is of great importance as it can help to re-evaluate the relevance of previous work for ecologically valid situations and may also be relevant for our understanding of psychiatric disturbances, which are often characterized by difficulties in social interaction rather than observation.

Conflict of interest

None declared.

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