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Current Opinion in Behavioral Sciences

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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Current Opinion in Behavioral Sciences 2015, **3**:130–135

This review comes from a themed issue on **Social behavior**

Edited by **Molly J Crockett** and **Amy Cuddy**

For a complete overview see the Issue and the Editorial

Available online 10th April 2015

doi:10.1016/j.cobeha.2015.03.006

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