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Reviews and perspectives

Neurocognitive mechanisms of gaze-expression interactions in face processing and social attention

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A B S T R A C T

The face conveys a rich source of non-verbal information used during social communication. While research has revealed how specific facial channels such as emotional expression are processed, little is known about the prioritization and integration of multiple cues in the face during dyadic exchanges. Classic models of face perception have emphasized the segregation of dynamic vs. static facial features along independent information processing pathways. Here we review recent behavioral and neuroscientific evidence suggesting that within the dynamic stream, concurrent changes in eye gaze and emotional expression can yield early independent effects on face judgments and covert shifts of visuospatial attention. These effects are partially segregated within initial visual afferent processing volleys, but are subsequently integrated in limbic regions such as the amygdala or via reentrant visual processing volleys. This spatiotemporal pattern may help to resolve otherwise perplexing discrepancies across behavioral studies of emotional influences on gaze-directed attentional cueing. Theoretical explanations of gaze-expression interactions are discussed, with special consideration of speed-of-processing (discriminability) and contextual (ambiguity) accounts. Future research in this area promises to reveal the mental chronometry of face processing and interpersonal attention, with implications for understanding how social referencing develops in infancy and is impaired in autism and other disorders of social cognition.

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A critical aspect of social cognition is the ability to accurately interpret the mental states, opinions and intentions of others. Schilbach and colleagues (Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008) use the term *intersubjectivity* to refer to the ability to convey and decode information in social interactions, which requires individuals to flexibly adapt to an ever-changing social environment. Dynamic facial cues, such as gaze direction and facial expression, are integrated with body gestures and prosody to allow humans and other higher primates to interpret the attentional focus and internal state of others during social interactions. During parenting, caregivers use attention-directing cues, such as pointing and head and gaze direction, in combination with prosody and facial expressions, to help infants determine whether it is appropriate to approach or avoid novel stimuli (*social referencing*) (Klinnert, Campos, Sorce, Emde, & Svejda, 1983). Humans and

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other primates living in complex social environments use gaze and expression to make inferences about the intentions and feelings of conspecifics that are relevant for survival and social integration (Klein, Sheperd, & Platt, 2009). Acute analysis of these fluid and nuanced nonverbal cues continue to be important for maintaining healthy relationships throughout the lifespan.

In addition to using social cues from gaze to identify the focus of another person's spatial distribution of attention in the environment, expression is used during social communication to interpret the emotional states of others and to predict their potential actions. When changes in emotional expression are combined with gaze shifts, the social cues of the partner provide additional information that directs one's actions toward or away from other stimuli in the environment. The role of gaze shifts is particularly important for some emotions, such as fear, where the meaning of the emotion is ambiguous until the source of the emotional change is discerned (i.e., to identify where the threat is located; Adams, Gordon, Baird, Ambady, & Kleck, 2003; Hadjikhani, Hoge, Snyder, & de Gelder, 2008; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007; Whalen et al., 2001). Thus, the combination of social signals like eye contact, gaze shifts and changes in emotional expression from a partner permits inferences regarding the internal state of the actor, and the salience of events in the environment and the dyadic context that can be powerful determinants of attention and action during social communication (e.g., Niedenthal, Mermillod, Maringer, & Hess, 2010).

The purpose of this review is to discuss recent research regarding the neural substrates of gaze and expression processing, and to examine theories regarding the integration of gaze and expression information in light of recent neuroimaging and behavioral studies. Although most of the recent work has been conducted in adults, the findings have important implications for understanding related developmental constructs like social referencing (Klinnert et al., 1983). The following sections will introduce and discuss classic models of face processing, theories regarding the integration of eye gaze and facial expression information, and recent research examining gaze and expression interactions, primarily in adults. Based on the evidence presented, we suggest that gaze and expression interactions are not obligatory and are only seen under certain conditions, and we discuss factors that might affect interactions between these two dimensions. Finally, we propose promising new directions for research.

1. Models of gaze and expression processing

Given the complexity and importance of face processing to social and emotional processing, considerable attention has been given to speculating about the cognitive and neural mechanisms that underlie the various aspects of face perception. An influential model of face processing (Bruce & Young, 1986) proposed that after a common low-level stage of encoding, information about the face is parsed into two distinct streams (Fig. 1). One stream processes view-independent aspects of faces, such as gender and identity whereas the other stream processes view-dependent aspects of faces, such as facial expression and gaze direction. Evidence supporting the independence of these streams has converged from a variety of sources including human behavioral studies (e.g., Prkachin & Prkachin, 1994; Young, McWeeny, Hay, & Ellis, 1986), human patient studies (e.g., Adolphs, Tranel, Damasio, & Damasio, 1994; Green, Turner, & Thompson, 2004) and single-cell studies in the macaque (e.g., Hasselmo, Rolls, & Bayliss, 1989).

Haxby, Hoffman, and Gobbini (2000, 2002) propose a similar model emphasizing the distinction between the processing of static and dynamic facial information (Fig. 1). Invariant facial information is processed in inferior regions of the temporal cortex, whereas dynamic information is processed in superior temporal regions, specifically in the superior temporal sulcus (STS). Furthermore, within each of these streams, more specific subtypes of face processing involve interactions of the stream-specific temporal lobe areas with other brain regions. For example, both gaze and facial affect perception are thought to engage the STS because they involve the detection of deviance in dynamic aspects of facial features (Haxby et al., 2000, 2002). However, gaze perception tends to elicit additional recruitment of the intraparietal sulcus (IPS), suggesting recruitment of the spatial attention system (Hoffman & Haxby, 2000; Pelphrey, Singerman, Allison, & McCarthy, 2003; Puce, Allison, Bentin, Gore, & McCarthy, 1998), whereas facial affect perception elicits additional activity in limbic structures, such as the amygdala and insula, depending to the category and/or intensity of emotion expressed (Adolphs et al., 1994; Phillips et al., 1997, 1998; Morris et al., 1998; Whalen, 1998; Whalen et al., 2001).

Consistent with the model by Haxby and colleagues, neuroimaging studies suggest that gaze processing and expression processing are subserved to some extent by common brain areas. In particular, there is evidence supporting the role of the STS in processing both gaze direction (Engell & Haxby, 2007; Hadjikhani et al., 2008; Hoffman, Gothard, Schmid, & Logothesis, 2007; Hoffman & Haxby, 2000; Hooker, Paller, Gitelman, Parrish, Mesulam, & Reber, 2003; Kingstone, Tipper, Ristic, & Ngan, 2004; Straube, Langohr, Schmidt, Mentzel, & Miltner, 2010) and facial expression (Engell & Haxby, 2007; Furl, van Rijsbergen, Treves, Friston, & Dolan, 2007; Hasselmo et al., 1989). A growing body of evidence also suggests that the role of the human amygdala is not exclusive to expression processing, but also includes processing gaze direction (e.g., Adams et al., 2003; Hadjikhani et al., 2008; Hooker et al., 2003; Kawashima et al., 1999; Sato, Kochiyama, Uono, & Yoshikawa, 2010; Sato, Yoshikawa, Kochiyama, & Matsumura, 2004; Straube et al., 2010). Electrophysiological studies in the macaque have also found evidence of face and gaze sensitive cells in the amygdala (Rolls, 1984). In a study with their amygdala-damaged patient S.M., Adolphs et al. (2005) concluded that her deficits in recognizing facial expressions stem from a failure to volitionally orient to information around the eye region. The sensitivity of the amygdala to the eye region is corroborated by the results of neuroimaging studies showing increased amygdala activation to the whites of the eyes (Kim, Somerville, Johnstone, Alexander, & Whalen, 2003; Kim et al., 2004; Whalen et al., 2004). In addition, patients with right unilateral amygdala damage have been shown to have deficits in integrating gaze and expression information in angry, fearful and happy faces (Cristinzio, N'Diaye, Seeck, Vuilleumier, & Sander, 2010). This review will focus on recent experimental evidence regarding the interactive or combined processing of these two types of dynamic facial information and the conditions under which such interactions might occur.

In spite of research suggesting that gaze direction and facial expression are processed in an integrated manner, other research suggests that gaze and expression are at least partially dissociable. For example, a high-resolution neuroimaging study of the macaque STS and amygdala (Hoffman et al., 2007) found evidence for separate gaze- and expression-sensitive areas with the amygdala: the basolateral amygdala was sensitive to threatening facial expressions whereas the central nucleus and areas of the stria terminalis were responsive to faces with averted gaze. These results converge with those of an fMRI study by Straube et al. (2010), who examined amygdala activity to static angry, happy and neutral faces with direct and averted gaze. While main effects of facial expression and gaze direction were found with respect to amygdala activity, no gaze and expression interactions were found, although gaze and expression interactions were seen in right STS in the form of enhanced activations for angry and happy faces with averted gaze. This is consistent with the finding that in macaques, overlapping regions of STS were responsive to both gaze direction and facial