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Reviews and perspectives

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

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ABSTRACT

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

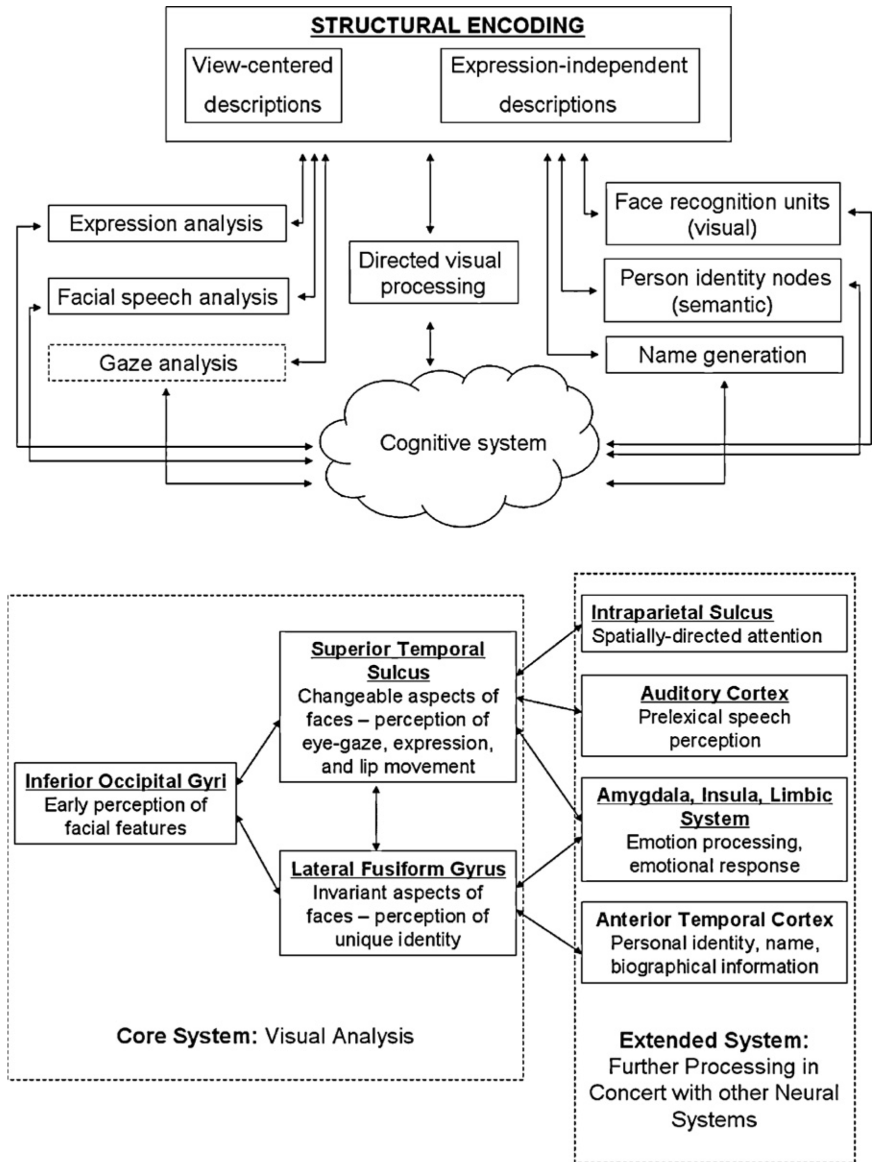

Fig. 1. Neurocognitive models of face processing. Top: Adapted with permission from Bruce and Young (1986). Bottom: Adapted with permission from Haxby et al. (2000). Note: Gaze analysis was not included in the original Bruce and Young model, but has been added here for theoretical context.

expression (Hoffman et al., 2007). STS activation to emotional gazing faces has also been examined in humans (Engell & Haxby, 2007). Expression sensitive areas of STS were anterior and inferior to areas sensitive to gaze shifts; however, overlapping areas of STS between these areas were responsive to both dimensions (Engell & Haxby, 2007).

Whereas neuroimaging studies have identified potential areas involved in the integration of expression and gaze direction and at least some dissociation in neural mediation of these facial attributes, studies examining the timing of gaze and expression processing suggest that these two dimensions may be processed in parallel pathways, at least during early visual analysis. Klucharev and Sams (2004) examined ERPs to happy and angry faces with direct and averted gaze. Different amplitude distributions for expression and gaze effects were observed such that happy expressions elicited larger P1 amplitudes primarily over centroparietal sites, whereas faces with direct gaze elicited larger P1 amplitudes over occipital areas. Gaze and expression interactions were not observed until 310 ms at various occipital, parietal and central sites in the P3 component. P3 amplitudes were enhanced to angry faces with direct gaze and happy faces with rightward gaze. These results converge with those from a transcranial magnetic stimulation study by Pourtois, Sander, Andres et al. (2004) and Pourtois, Sander, Grandjean, and Vuilleumier (2004), who applied TMS over STS and somatosensory cortex during the early stages of face processing (100 and 200 ms after face presentation). Stimulation of STS selectively disrupted gaze processing, while stimulation of somatosensory cortex selectively disrupted expression processing. Together, these two studies suggest that gaze and expression could be initially processed in parallel independent pathways.

2. Theories of gaze and expression interactions: direct gaze, appraisal, and shared signals

Neuroanatomical and neuroimaging studies suggest that there is at least partial overlap in the systems that process gaze and expression. Nevertheless, the degree and nature of the interaction between gaze and expression processing remains uncertain – exactly how or why would these two dimensions interact? Theories regarding such interactions share similarities in their emphasis on the perceived significance of a given combination of gaze and expression for the observer (e.g., self-relevance). A fundamental assumption of these theories is that gaze and expression information are integrated by the observer to form expectations or inferences about the internal state and intentions of the performer, suggesting that the presence of multiple face cues triggers appraisal processes that in turn, affect how we respond to different combinations of facial expression and gaze direction. Although there is debate as to whether facial movements are necessarily tied to genuine emotions or perform social communicative functions (e.g., Ekman, 1997; Parkinson, 2005), here we consider only those situations in which expression and gaze direction may serve a communicative role during dyadic exchanges.

One theoretical perspective argues for a specialized role for direct gaze in the perception of facial expression (*direct gaze hypothesis*) (e.g., Senju & Hasegawa, 2005). Averted gaze signals the intention of the gazer away from the perceiver whereas direct gaze is directed toward the perceiver, resulting in the feeling of being "looked at". As such, expressive faces with direct gaze should be more self-relevant than those with averted gaze, and this feeling of being looked at results in the enhancement of all aspects of face processing, including the processing of facial expression (Senju & Hasegawa, 2005). For example, evidence suggests that direct gaze is processed more quickly than averted gaze and has an effect on judgments involving other aspects of face processing, including facial attractiveness (Kampe, Frith, Dolan, & Frith, 2001) and gender discrimination (McCrae, Hodd, Milne, Rowe, & Mason, 2002; but see Vuilleumier, George, Lister, Armony, & Driver, 2005 for evidence that gender judgments are faster for faces with averted gaze). Notably, neuroimaging evidence suggests that direct gaze may engender heightened processing of emotional expressions, in that anterior STS activity is enhanced during the presentation of emotional faces with direct gaze (Wicker, Perrett, Baron-Cohen, & Decety, 2003). Neuroimaging research by Schilbach et al. (2006) further suggests that the sense of self-relevance signaled by direct gaze might be linked to activity in dorsomedial prefrontal cortex. This view regarding the salience of self-relevance as signaled by direct gaze runs counter to findings of increased amygdala activations to expressive faces with averted gaze in the macaque, which indirectly suggests that faces with averted gaze are potentially more emotionally arousing than those with direct gaze (Hoffman et al., 2007).

Alternatively, Sander and colleagues (Sander et al., 2007) argue that the decoding of facial expression is performed by inferring the appraisal pattern of the expressor from observable facial cues like gaze and expression (*appraisal hypothesis*). Thus, the behavioral relevance of specific combinations of gaze and expression should modulate the interactions between the two dimensions. For example, angry faces should be more relevant to an observer if they are making eye contact, since this could imply that an attack is imminent. On the other hand, Sander et al. (2007; see also Adams & Kleck, 2003) argue that fearful faces with averted gaze should be more behaviorally relevant than those with direct gaze, since this combination of dimensions could signal the presence of a potential threat in the immediate peripheral environment (e.g., Sander, Grafman, & Zalla, 2003). Consistent with this notion, Sander et al. (2007) found that angry faces were recognized as more angry when their gazes were directed at the observer, while fearful faces were rated as more fearful when gaze was averted. This pattern of results was replicated by N'Diaye, Sander, and Vuilleumier (2009) who also observed increased activity in the amygdala, as well as in fusiform and medial prefrontal areas to directly gazing angry faces and fearful faces with averted gaze. However, this pattern of results was only observed for low-intensity and not high-intensity facial expressions. This integration of expression and gaze was also observed in healthy controls in a subsequent study (Cristinzio et al., 2010), but not in patients with right amygdala damage, and to a lesser extent in individuals with left amygdala damage.

Adams and Kleck (2003, 2005) propose that gaze and expression are processed in an integrated manner, such that direct gaze facilitates the processing of approach-oriented emotions (joy and anger), whereas averted gaze facilitates avoidance-related emotion processing (sadness and fear). According to the *shared signal hypothesis* (Adams & Franklin, 2009), these combinations of gaze and expression share congruent signal value in terms of approach and avoidance tendencies, and therefore should be processed more efficiently. The amygdala is thought to play a role in this effect (Adams et al., 2003). In accordance with this view, Hooker et al. (2003) reported that STS activation to averted gaze was modulated by facial expression, being greater for angry faces than happy faces, perhaps due to the conflict in motivational tendencies for angry faces with averted gaze. In other words, both happy and angry faces with direct gaze act as approach signals on the part of the expressor; however, directly gazing happy faces tend to elicit approach behaviors and directly gazing angry faces may elicit avoidance behaviors on the part of the observers. We note, however, that anger could elicit approach tendencies in the observer in situations where confronting the aggressor is likely to yield a beneficial outcome (see Harmon-Jones, 2003, for a review).

Although the theories described above differ somewhat in their specific predictions regarding gaze and expression interactions, the appraisal and shared signal hypotheses seem to imply that such interactions are inevitable, and that gaze and expression will always be processed in an integrated manner. However, recent reviews of gaze and expression interactions indicate that the interactivity of these two dimensions is probably moderated by various factors, including discriminability, processing speed, individual differences in culture and personality, and top-down influences that arise as a consequence of factors like context and expectation (Adams, Franklin, Nelson, & Stevenson, 2010; Adams & Nelson, 2011).While the aforementioned studies have focused on how gaze direction may modulate the perception of facial expression, recent studies have also focused on how facial expressions moderate the perception of gaze direction. Gaze direction judgments are faster overall in fearful faces with averted gaze and angry faces with direct gaze (Adams & Franklin, 2009). Interestingly, these interactions were most pronounced in slow responders, a result that will be discussed in greater detail in subsequent sections. Lobmaier, Tiddeman, and Perrett (2008) found that happy faces were most likely to be perceived as looking directly at the observer, and that angry faces were more likely to be perceived as looking directly at the observer than fearful or neutral expression. Converging with these studies, Ewbank, Jennings, and Calder (2009) reported that angry faces were more likely to be perceived as looking directly at the observer than fearful or neutral faces and that this effect was abolished when faces were inverted.

In spite of these studies, mounting behavioral evidence suggests that gaze and expression processing only interact under certain conditions. For example, Bindemann, Burton, and Langton (2008) examined the effect of task demands on gaze and expression interactions as predicted by Adams and Kleck (2003), in order to determine whether integration of these two dimensions occurs at early processing stages. While they were able to replicate Adams and Kleck's (2003) observation of enhanced processing for fearful/sad expressions with averted gaze and happy/angry expressions with direct gaze in one study using the same task and similar stimuli (Experiment 5), they observed impairments in categorizing all expressions with averted gaze when using speeded classification tasks (Experiments 1, 2, 3, and 6), as well as lower emotional intensity ratings for fearful faces with averted gaze using a ratings task. These results are indicative of a processing advantage for directly gazing faces under most circumstances, in support of direct gaze hypothesis. It is important to note, however, that there were differences in the actual stimuli used by Bindemann et al. (2008) and Adams and Kleck (2003). Whereas the former study used 5 models, each portraying 6 different expressions from Ekman and Friesen's (1976) Pictures of Facial Affect, the latter used 30 distinct stimuli (30 different models depicting 6 different expressions). These stimulus differences may have played a role in the discrepant results, which will be discussed further in subsequent sections. Using an attentional blink paradigm, Milders, Hietanen, Leppänen, and Braun (2011) found that fearful faces were detected more frequently with averted gaze than with direct gaze, whereas happy and angry faces were detected more frequently with direct gaze, supporting the appraisal and shared signal hypotheses. Taken together, the results of these studies suggest that interactions between gaze and expression processing are sensitive to stimulus and task demands.

3. Garner selective attention paradigm: speed-of-processing and contextual ambiguity

Qualified interactions between gaze and interaction have also been observed with the Garner two-choice speeded-classification task (Garner, 1974, 1976), which allows for the determination of whether two stimulus dimensions interact and whether they are processed independently or in an integrated manner. The logic underlying the Garner paradigm is that if two stimulus dimensions are processed integrally, it will be impossible to attend to one dimension and ignore the other. Instead, variations in the irrelevant dimension should cause interference that creates performance deficits, commonly manifested as slowed reaction times. For example, if gaze and facial expression processing are processed in an integrated manner, it should be difficult to attend to gaze and ignore facial expression, and vice versa.[1]

The relationship between gaze and expression has been examined with the Garner paradigm (Ganel, 2011; Ganel, Goshen-Gottstein, & Goodale, 2005; Graham & LaBar, 2007). In Ganel and colleagues' (2005) first experiment, participants classified faces either with respect to gaze direction (direct vs. right, or left vs. right) or their facial expression (happy vs. angry) and ignored the irrelevant dimension. Overall, reaction times were slower for emotion judgments, suggesting that emotion was less discriminable than gaze (Algom, Dekel, & Pansky, 1996). Garner interference (GI) was present in both the gaze and emotion tasks. That is, longer reaction times in the orthogonal condition relative to the control condition were evidenced for both types of judgments. In their second experiment, Ganel et al. (2005) examined the effect of face inversion on gaze and emotion judgments and, in addition to finding that emotion judgments still took longer than those for gaze, they found that the gaze no longer interfered with emotion but emotion still interfered with gaze. Their third experiment equated the two tasks for disciminability by increasing the difficulty of the gaze task relative to the emotion task (direct vs. 20° left-averted, 20° vs. 40° left-averted gaze). This manipulation created asymmetric interference effects – gaze interfered more with emotion judgments than emotion with gaze judgments. The authors interpreted these effects in the context of configural vs. featural processing: whereas expression processing is configural, entailing an obligatory computation of gaze direction, gaze processing is feature- or part-based and relies more on local features.

In a subsequent study using the Garner task, Ganel (2011) examined the role of head direction on gaze and expression interactions using fearful and angry faces. In Experiment 1A, head orientation was kept constant and GI was observed, replicating the results of Ganel et al. (2005). However, when head orientation varied in Experiment 1B, performance was similar across the baseline and orthogonal blocks, suggesting that expression and gaze were processed as separate dimensions. In contrast, head orientation did not affect interactions between expression and identity (Experiment 2A and 2B). The explanation offered for these findings was that the introduction of head direction in Experiment 1 reduced the necessity of featural level analyses (i.e., the position of the irises) in determining gaze direction. Instead, the introduction of head direction required that computation of gaze direction be based on both the position of the irises and the global orientation of the head, which may have disrupted GI. In contrast, because the extraction of identity relies more on viewer-independent processes (Bruce & Young, 1986), viewer-centered attributes like head orientation should have less influence, leading to GI in processing identity and expression.

Graham and LaBar (2007) examined whether the Garner task would provide evidence of gaze and emotional expression interactions similar to those found in other studies, and whether stimulus discriminability would have an influence on Garner interference. While Ganel et al. (2005, Experiment 1) reported a symmetric pattern of GI for gaze and emotional expression, coupled with an overall reaction time advantage for gaze judgments, Graham and LaBar (2007, Experiments 1 and 2) found asymmetric GI effects, such that while expression interfered with gaze judgments, gaze did not interfere with emotion judgments. This finding was accompanied by an overall reaction time advantage for emotion judgments, suggesting that when emotion is easily resolved, it is processed before gaze can interfere. The results of Experiments 3 and 4 further showed that when the difficulty of the emotional expression discrimination was increased, the reaction time advantage for emotion judgments disappeared and a symmetrical pattern of GI resulted.

These findings are important because they suggest that the idea of a single, integrated system mediating gaze and expression is oversimplified. Instead, the fact that relationships between gaze and expression, as indexed by GI, can be manipulated by inversion or discriminability implies that integrated processing of these two facial dimensions only occurs under certain circumstances. While the results of Ganel et al. (2005) and Graham and LaBar (2007) suggest that the degree to which expression and gaze interact depends critically on their baseline discriminability, the mechanism underlying these effects is unclear. One possibility is that discriminability effects support a *speed-of-processing account* of gaze and emotional expression interactions. When emotional expression was easily discriminable (Graham & LaBar, 2007, Experiments 1 and 2), it occurred before gaze could interfere; however, when emotional expression was difficult to discriminate (Experiments 3 and 4), processing slowed and gaze information interfered with emotion judgments. When gaze discrimination was easier than emotion discrimination (as in Ganel et al., 2005), the processing advantage for emotional expressions was reversed and a symmetric pattern of interference was observed. Notably, when Ganel et al. (2005) made their gaze discrimination task more difficult (Experiment 3), they observed an asymmetrical pattern of GI that was caused by

[1] Garner interference (GI) is determined by comparing performance across two conditions: a control or baseline condition where only the relevant dimension varies and the irrelevant dimension is held constant, and an orthogonal or filtering condition where both dimensions vary (Ashby & Maddox, 1994; Maddox & Ashby, 1996). GI occurs when variations in the irrelevant dimension cause slowed responding or decreased accuracy in judgments of the relevant dimension and supports the conclusion that two dimensions are processed in an integrated fashion. The Garner paradigm has been used to study the interdependence of various aspects of face processing, including the relationship between gender and identity (Ganel & Goshen-Gottstein, 2002), gender and emotional expression (Atkinson, Tipples, Burt, & Young, 2005), identity and expression (Baudouin, Martin, Tiberghien, Verlut, & Franck, 2002; Schweinberger, Burton, & Kelly, 1999; Schweinberger & Soukup, 1998), and identity and speech information (Schweinberger et al., 1999; Schweinberger & Soukup, 1998).

emotion interfering with gaze judgments more than gaze interfered with emotion judgments. This speed-of-processing account is also supported by Adams and Franklin's (2009) finding of that gaze and expression interactions in a gaze detection task are moderated by processing speed – individuals with slower processing speeds (as indexed by reaction time) showed evidence of greater gaze and expression interactions.

An alternative explanation (*contextual account*) could be that altering the discriminability of a dimension could increase or decrease ambiguity regarding information in the face. In other words, when information along one dimension is ambiguous (e.g., facial expression), social observers might turn to other information (e.g., gaze direction) to help resolve the ambiguity. However, if information along one dimension is easy to resolve, there is no need to integrate additional information. For example, Graham and LaBar (2007) found that when emotional expressions were easily discriminable (Experiments 1 and 2), there was no evidence of gaze/expression interactions. In contrast, when the emotion discrimination was made more difficult, gaze and emotion interactions emerged that were similar to those reported previously (Adams & Kleck, 2003, 2005; Sander et al., 2007). In Experiment 3, when subtle facial expressions were employed, gaze and emotional expression interactions were observed as an advantage for faces with direct gaze, especially angry ones. In Experiment 4, when commonly confused facial expressions were used, this interaction was similar to that evidenced in Experiment 3: there was a processing advantage for faces with direct gaze, in particular for directly gazing surprised faces. It is important to note that factors other than discriminability might also contribute to ambiguity. For example, according to appraisal and shared-signal accounts of gaze and expression processing, certain combinations of gaze and expression may produce ambiguity with regard to the intentions of the actor. This aspect of ambiguity is discussed further in subsequent sections. In summary, GI studies provide additional evidence that a single unitary system underlying gaze and expression processing is oversimplified. Factors such as task differences (including the role of global and local features in making task-related responses) and baseline discriminability modulate the degree to which these two features interact.

4. Effects of expression on social attentional orienting: gaze cuing paradigms

The neuroimaging literature suggests that there is some overlap in the brain areas that subserve expression and gaze perception, while behavioral evidence is indicative of at least some integrated processing of these two facial dimensions. Therefore, it is reasonable to expect that reflexive orienting to gaze would be modulated by facial expression. Reflexive orienting to gaze is shown in gaze-cuing studies, which have reliably shown individuals will automatically shift their attention to gazed-at locations, even if they are told that gaze direction does not predict the location of the target (e.g., Friesen & Kingstone, 1998; see Frischen, Bayliss, & Tipper, 2007 for a review). This phenomenon has been demonstrated in both humans (Deaner & Platt, 2003; Driver et al., 1999; Friesen & Kingstone, 1998, 2003a, 2003b; Friesen, Moore, & Kingstone, 2005; Friesen, Ristic, & Kingstone, 2004; Hietanen, 1999; Langton & Bruce, 1999; Ristic, Friesen, & Kingstone, 2002; Ristic & Kingstone, 2005) and non-human primates in certain behavioral contexts (Deaner & Platt, 2003; Emery, Lorincz, Perrett, Oram, & Baker, 1997; but see Itakura, 1996; Tomonaga, 2007; Tomasello, Hare, Lehmann, & Call, 2007), suggesting that gaze is an evolutionary important form of communication in higher primates. Intuitively, it makes sense that gaze and expression could interact to direct attentional orienting. For example, if one were to encounter a fearful individual looking in a particular direction, one would quickly shift attention to where the other was looking, since a significant and potentially threatening event might be occurring in that location. Reacting adaptively to this sort of situation would require the integration of gaze and expression information, engaging brain areas like the STS and amygdala that are part of a processing stream that is sensitive to both gaze and expression information.

The notion that fearful and angry faces can act as signals of threat, and as such should be particularly salient, has been examined in neuroimaging studies in both adults and infants (but see Brosch, Sander, Pourtois, & Scherer, 2008). For example, a wealth of evidence suggests that angry faces capture attention (e.g., Fox et al., 2000; Öhman, Lundqvist, & Esteves, 2001;Wilson & MacLeod, 2003), especially in highly anxious individuals (e.g., Bradley, Mogg, & Millar, 2000; Fox, Mathews, Calder, & Yiend, 2007; Mogg, Phillipot, & Bradley, 2004). Angry faces with direct gaze also elicit an enhanced Nc ERP component (thought to be an index of attentional orienting) in 4- and 7-month old infants (Hoehl & Striano, 2008; Striano, Kopp, Grossman, & Reid, 2006). Fearful faces, particularly those with averted gaze, are thought to act as a threat signal and capture attention similarly (Mogg, Garner, & Bradley, 2007). Fearful faces elicit an enhanced N290 ERP component in 7-month old infants (Hoehl & Striano, 2008) and have been shown to enhance subsequent target processing in adults (Pourtois, Sander, Grandjean et al., 2004). Fearful faces with averted gaze elicit activations in brain areas associated with shifts of attention (IPS) and additional regions associated with biological motion and emotion perception, including the amygdala and STS (Hadjikhani et al., 2008). Enhancement of the processing of targets cued by fearful faces has been linked to modulations in IPS and extrastriate activity (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2006).

To date, attempts to demonstrate *behavioral* interactions between gaze cuing effects and expression effects have produced mixed results (see Graham, Friesen, Fichtenholtz, & LaBar, 2009 for a detailed review). In some of these studies, either no effect of expression on gaze-triggered orienting was observed (e.g., Hietanen & Leppänen, 2003), or an effect was observed, but only in a subset of subjects (e.g., anxious participants, Mathews, Fox, Yiend, & Calder, 2003). Collapsing across subjects ranging from low to high in trait fearfulness, Tipples (2006) found a larger gaze cuing effect for fearful faces than for neutral faces, but contrary to what one might expect, he found no difference between fearful and happy faces. In contrast, Putman, Hermans, and van Honk (2006) found larger gaze-cuing effects across participants for fearful faces compared with happy faces at a short SOA of 100 ms. Graham et al. (2009, Experiments 5 and 6) also observed the same effect, but only at a longer SOA of 525 ms and not at 225 ms; however, it was observed in only one of two similar experiments.

Using dynamic facial displays that controlled for local changes in eye aperture during the gaze shift, Graham et al. (2009) demonstrated that expression and gaze information have separate effects on target detection and identification in Posner-style cuing tasks when a short interval intervenes between the gaze shift and the appearance of the target. When a face was emotional, participants detected and identified targets more quickly than when the face was neutral, regardless of where the eyes were looking. This effect was independent of reflexive orienting to gaze direction, where participants were faster to detect and identify targets that were validly cued by eye gaze. One interpretation of this finding is that if individuals have time to process the cue more fully, the two kinds of information can interact to influence visual orienting.

Gaze-cued orienting has also been examined with ERPs to reveal temporal sequencing effects that are difficult to resolve with behavioral studies. ERP studies of gaze-directed attentional orienting using neutral face cues have demonstrated enhanced P1 amplitude in response to gazed-at targets (valid) compared to targets presented across the screen from the gazed at location (invalid), and greater P3 amplitude in response to invalid compared to valid targets (Schuller & Rossion, 2001, 2004, 2005). An ERP study with emotional faces (Fichtenholtz, Hopfinger, Detwiler, Graham, & LaBar, 2009) revealed several sequential ERP effects to neutral targets (a checkerboard stimulus): (1) an early enhancement of target processing following fearful faces evident in the P1 component thought to index early visual processing, (2) a later interaction between expression and gaze reflected in the N1 component that was indicative of enhanced target processing following fearful faces with rightward gaze, and (3) an even later interaction between gaze and target location reflected in the P3 that was suggestive of enhanced processing for invalidly cued left visual field targets. Behaviorally, participants responded faster to targets following fearful faces and targets presented in the right visual field, in concordance with the P1 and N1 effects, respectively.

Similar studies have also been conducted with infants as young as 3 months of age (e.g., Hoehl & Striano, 2008). The frontocentrally distributed Nc component, thought to reflect attentional orienting, is sensitive to gaze and expression combinations, being to enhanced to objects cued by fearful (Hoehl & Striano, 2008; Hoehl, Wiese, & Striano, 2008) and angry faces (Hoehl & Striano, 2008) relative to happy faces, suggesting that even very young infants are sensitive to combinations of facial expression and gaze direction and will allocate increased attentional resources to toward objects that could be potentially dangerous. These findings are consistent with the shared-signal and appraisal hypotheses, which posit that threat-related social signals should be processed more efficiently.

The findings of Fichtenholtz et al. (2009) indicate that facial expression and gaze direction modulate attentional orienting across different temporal stages of processing, in accordance with a speed-of-processing account of gaze and expression interactions. These findings suggest that the effects of gaze and expression on subsequent attentional orienting are spatiotemporally dissociable: facial expression took precedence over gaze direction with respect to its effects on target processing, suggesting that evaluating another individual's emotional state may be initially more important during shared attention compared to where someone is looking. However, it is important to note that unambiguous facial expressions were used in this study, making it difficult to rule out the possibility that ambiguity is an important factor in interactions between these two stimulus dimensions. On the other hand, the infant research is suggestive of a more contextual explanation for these interactions. It is important to note that gaze cuing studies have examined ERPs to targets rather than face cues, which may have tapped into processes associated with attentional allocation that arose as a result of processing interactions occurring at the level of the facial cue, rather than activity in response to the cue itself.

The incongruous results across and within gaze-cuing studies to date suggest that the effect of expression on gaze-triggered orienting is tenuous. One reason could be that there is considerable variation in the timing of stimulus presentation across these studies, in terms of gaze cue and expression presentation, and in terms of cue-target stimulus onset asynchronies (SOAs). For example, some studies used cuing sequences that may have minimized perceived cue-target contingencies (e.g., the face displays an emotion and then gazes to the side) and some may have presented the target too soon (i.e., before gaze and expression information could be integrated). However, weak or absent interactions between gaze and expression may have also been due to the lack of context in which the gaze and expression cues were presented.

In the cuing studies reviewed above, targets were always emotionally neutral (e.g., expressive faces repeatedly looked toward locations where emotionally neutral objects such as symbols or checkerboards might subsequently appear). It is possible that for expression processing to be fully engaged in such experiments (i.e., for expression to have an optimal effect on gaze-triggered orienting), it might be necessary to present targets that would logically elicit emotional expressions in a gazing face. For example, when a participant is presented with a fearful gazing face, it might matter that an upcoming target could be threatening, such as a man with a gun or an attacking dog.

In support of this notion, a recent study using emotionally valenced words as targets observed gaze-cuing effects for fearful and disgusted faces (and not for happy and neutral faces) when participants evaluated target words as positive or negative (Pecchinenda, Pes, Ferlazzo, & Zoccolotti, 2008). When a separate group of participants judged whether the same target words were in upper or lower case letters, there were equivalent cuing effects for all expressions and cuing effects for the negative expressions were significantly smaller relative to the evaluative task. Thus, the enhancement of attentional orienting to gazing faces with negative expressions may require that participants be engaged in a task involving an explicit evaluation of target valence. This conclusion is consistent with a study by Bayliss, Frischen, Fenske, and Tipper (2007) in which participants gave more positive evaluations to neutrally valenced household objects that had been gazed at by a happy face compared with a disgusted face.

The possibility that the use of meaningful targets would give rise to enhanced orienting to fearful gazing faces has also been examined with valenced and neutral targets (Friesen, Halvorson, & Graham, 2011). To this end, nonpredictive directional gaze cues were presented in a face whose expression changed from neutral to either fearful or happy, followed by a target that was either emotionally valenced (Friesen et al., 2011, Experiment 1) or emotionally neutral (Experiment 2) at both short and long SOAs. With the emotionally valenced targets, clear evidence of both gaze processing and expression processing effects at the short SOA were observed, but no interaction between the two. Evidence of the integration of gaze and expression information was observed at the long SOA, with enhanced gaze cuing effects for fearful faces, converging with the results of several neuroimaging studies that have suggested that gaze direction information and emotional expression information are dissociable, at least at early stages of processing (e.g., Fichtenholtz et al., 2009; Klucharev & Sams, 2004; Pourtois, Sander, Andres et al., 2004; Pourtois, Sander, Grandjean et al., 2004). In contrast, Experiment 2 (Friesen et al., 2011) used an identical cuing sequence but with emotionally neutral targets, and found that the interaction between gaze cuing and expression was only marginally significant and that these factors did not interact with SOA as they had in Experiment 1. This result suggests that although the cuing sequence may have enhanced the effect of facial expression on gaze cuing, the presentation of meaningful targets in Experiment 1 was important. This result seems counter to those reported by Graham et al. (2009, Experiments 5 and 6) where enhanced cuing was observed for fearful gazing faces compared with happy gazing faces in one experiment using meaningless targets, but not another. These mixed findings suggest that integration of gaze and expression information can sometimes occur in the absence of meaningful targets. In a related study using an oculomotor visual search task, Kuhn and Tipples (2011) examined whether gaze would interact with fearful or happy expression when participants were required to search for threatening or pleasant targets. While an advantage for gazing fearful faces was observed for threatening targets, this advantage disappeared for pleasant targets. Together, these studies suggest that contextual factors such as the use of meaningful targets and task demands may be particularly important in determining interactions between gaze and expression.

Fichtenholtz, Hopfinger, Detwiler, Graham, and LaBar (2007) used ERPs to compare the effects of multiple facial expressions on the processing of peripherally presented emotionally salient targets during a gaze-cuing task. Early processing benefits were found for facial expression cuing. P130 amplitude, maximal over contralateral occipital sites, was greatest in response to targets following happy faces. Emotional target effects emerged later in the P3 complex, presumably when target identity is integrated into the socioemotional context set up by expectancy. P3 effects were characterized by reduced peak latency to the positive target (baby), particularly in the right visual field. Fearful expression reduced parietally distributed P3 amplitude for gazed-at targets (cue emotion × gaze validity), providing evidence for the presence of spatially directed attention. Behavioral results validated that attention was effectively manipulated by the gaze-cuing paradigm. The majority of effects were driven by positive emotion but were not spatially directed, consistent with the idea that happy expressions in social exchanges set up global expectations for possible rewarding outcomes that induce approach-oriented motivational states and broaden attentional focus. In contrast, fearful expressions facilitated the spatial direction of attention cued by eye gaze as manifested in a centrally distributed negativity (N180), in accordance with its social role in communicating the detection of a specific threat in the local environment. Converging with Fichtenholtz et al. (2009), these results suggest that the deployment of attention by observing multiple dynamic facial signals in others emerges over sequential processing stages and can be distinguished from effects driven by the emotional significance of environmental stimuli. Again, it is important to note that unambiguous facial expressions were used in this study, making it difficult to rule out the possibility that ambiguity may be an important factor in interactions between these two stimulus dimensions. In addition, this study also examined ERPs to targets rather than cues, which may have tapped into attentional processes that arose as a result of processing interactions occurring at the level of the facial cue.

5. Conclusions

Given the rich capacity for social interactions in humans and higher primates, the mechanisms by which the emotional states and intentions of others are decoded are undoubtedly complex. It has been proposed that humans construe intentions through the actions of others, with the assumption that these actions are a manifestation of another's goals, preferences, attention and knowledge (Phillips, Wellman, & Spelke, 2002). Information from the face, such as expression and gaze direction, can provide important clues to others' intentions. The overall picture arising from the results from studies examining interactions between facial expression and gaze direction is one of mixed results that appear to be highly dependent on the stimuli used (e.g., static vs. dynamic, schematic vs. real), the relative timing and order of gaze and expression changes, and the task demands involved. A complete account of these processes and how they are ultimately integrated and affect subsequent behavior must include the moderating influences of time- or stimulus-dependent factors and their interactive effects on social cognitive functions such as theory of mind or joint attention.

5.1. Face processing models, revised

According to Bruce and Young's (1986) early model of face processing, view-centered descriptions like gaze direction, expression, and lip movement related to speech are processed in parallel with expression independent descriptions like identity and gender and therefore, should not interact. Similarly, the model of Haxby and colleagues (2000, 2002) posits that 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). However, studies using the Garner task (e.g., Atkinson et al., 2005; Baudouin et al., 2002; Schweinberger et al., 1999; Schweinberger & Soukup, 1998) strongly suggest that these kinds of information can interact.

The notion of qualified interactions between gaze and expression has implications for psychological and neurobiological models of face processing, which have traditionally considered emotion and gaze together as part of a dynamic featural processing stream. In particular, the idea that view-centered descriptions or changeable aspects of faces are processed in an integral fashion requires some revision. According to Haxby et al. (2000, 2002), dynamic information from faces is thought to engage primarily the STS. Gaze perception should elicit additional recruitment of the IPS, due to the recruitment of the spatial attention system (e.g., Hoffman & Haxby, 2000; Pelphrey et al., 2003; Puce et al., 1998), whereas expression perception should elicit additional activity in limbic structures such as the amygdala (e.g., Adolphs et al., 1994; Morris et al., 1998; Phillips et al., 1997, 1998; Whalen, 1998; Whalen et al., 2001). However, experimental evidence suggests that while the STS may be involved in processing both kinds of information, they are not always processed in an integral manner and may be processed, at least initially, in separate streams (e.g., Klucharev & Sams, 2004; Pourtois, Sander, Andres et al., 2004; Pourtois, Sander, Grandjean et al., 2004). Consistent with this idea, Engell and Haxby (2007) found that expression sensitive areas of STS were anterior and inferior to areas sensitive to gaze shifts; however, intermediate sectors of STS were responsive to both dimensions. Furthermore, Adams and colleagues (Adams, Franklin, Nelson et al., 2011) reported activation of different STS regions while processing angry gazing faces as a function of stimulus duration, suggesting that STS regions may be involved in processing gaze and expression at different stages of processing, possibly via reentrant volleys. Further research is necessary in order to characterize exactly how these dimensions are processed by relatively early (preattentive/reflexive) and later (reflective) visual mechanisms.

According to Haxby et al. (2000, 2002), the primary role of the amygdala was thought to be its role in resolving facial expression. However, as reviewed earlier, several neuroimaging studies have also strongly implicated this structure in processing both expression and gaze (e.g., Adams et al., 2003; Hadjikhani et al., 2008; Hooker et al., 2003; Kawashima et al., 1999; N'Diaye et al., 2009; Sato et al., 2010, 2004). Nevertheless, it is important to note that not all studies have found this result (e.g., Straube et al., 2010) and that while these studies do implicate the amygdala in both gaze and expression processing, across studies, exact results have been mixed. For example, while Adams et al. (2003) found increased amygdala activation to angry faces with averted gaze and fearful faces with direct gaze, Hadjikhani et al. (2008) and Sato et al. (2004) observed the opposite pattern: increased amygdala activation to directly gazing angry faces and averted fearful faces. A similar pattern was also found by N'Diaye et al. (2009), but only for low-intensity facial expressions. Furthermore, while Sato et al. (2010) observed increased activity to happy and angry faces with direct gaze, this was only in response to dynamic, not static, faces. Finally, high resolution imaging of the macaque amygdala (Hoffman et al., 2007) indicates some dissociation between areas of the amygdala associated with processing gaze (i.e., stria terminalis) and expression (i.e., basolateral amygdala). Explanations for these discrepant findings include the nature of the stimuli used (e.g., static vs. dynamic faces), how gaze direction was derived (e.g. via head direction or iris position), the temporal sequence of gaze and expression changes (e.g., whether the gaze shifts occurred prior to the expression change or simultaneously). High resolution imaging of the human amygdala during gaze and expression processing may provide answers to these questions. Regardless of the exact nature of these interactions, the majority of evidence points to the conclusion that the amygdala's role extends beyond that of basic emotion recognition or arousal processing and that it may be an integral part of an appraisal system that is sensitive to shared signals or self-relevance as signaled by conjoint consideration of expression and gaze direction, among other features.

5.2. Theoretical accounts

Overall, the review of the extant literature on gaze and expression interactions suggests that the systems processing these dimensions can operate independently, although they may share some overlapping functions. Because of this, these two kinds of information may only interact under certain conditions. At the present time, there are several possible explanations for the mixed results observed regarding gaze and expression interactions, including speed-of-processing accounts, the role of ambiguity, the nature of task demands and stimuli used, and the role of individual differences. These will be discussed in turn below.

One possibility is that gaze and expression interactions may or may not interact, depending on the relative ease at which these dimensions are discriminated (i.e., a *speed-of-processing account)*. Given that gaze and expression may initially be processed in separate streams (Klucharev & Sams, 2004; Pourtois, Sander, Andres et al., 2004; Pourtois, Sander, Grandjean et al., 2004), and may be subserved by different areas of the amygdala (Hoffman et al., 2007) and STS (Engell & Haxby, 2007; Adams, Franklin, Nelson et al., 2011), if one or both of these dimensions is easily resolved, then processing should occur quickly and in separate streams. However, if either discrimination is difficult, processing is slowed and interactions between the two dimensions results. Evidence in favor of this notion comes primarily from experiments examining GI, which is sensitive to stimulus discriminability (Garner, 1976). For example, Graham and LaBar (2007) found that when emotional expression was easily discriminable, it occurred before gaze could interfere; however, when emotional expression was difficult to discriminate, processing slowed and gaze and expression interactions were evidenced. Similarly, Ganel et al. (2005) demonstrated that when gaze discrimination was easier than emotion discrimination, a processing advantage for emotional expressions was not observed and a symmetric pattern of interference was observed. However, when the gaze discrimination task was more difficult, an asymmetrical pattern of GI was observed that was caused by emotion interfering with gaze judgments more than gaze interfered with emotion judgments. This speed-of-processing account is also supported by Graham et al. (2009) and Friesen et al. (2011), who only observed interactions between gaze and expression in a gaze cuing study at longer SOAs, and Adams and Franklin's (2009) finding that only individuals with slower reaction times to identify gaze direction showed enhanced gaze and expression interactions. Studies employing event-related potentials, especially those using the Garner task, may help to determine whether a speed-of-processing account provides the best account of gaze and expression interactions.

Related to the notion of discriminability, an alternative determinant of gaze and expression interactions could be that altering the ease with which a dimension can be resolved will increase or decrease ambiguity regarding information in the face (i.e., *a contextual account*). Evidence suggests that human observers resolve facial expressions efficiently, integrating information about feature displacement from the eyes downward and stopping when enough information to identify and emotion has been integrated (Schyns, Petro, & Smith, 2007). However, it is possible that if facial expression cannot be discriminated from feature displacement alone, information regarding eye gaze may be used to resolve ambiguity. Consistent with this account, N'Diaye et al. (2009) observed gaze and expression interactions in the form of heightened amygdala activity for fearful faces with averted gaze and directly gazing angry faces, but only for low intensity emotions. Graham and LaBar (2007) found that when emotional expressions were easily discriminated, there was no evidence of gaze/expression interactions; however, when the emotion discrimination was made more difficult, gaze and emotion interactions emerged that were similar to those reported previously (Adams & Kleck, 2003, 2005; Sander et al., 2007). Ambiguity may also be created by specific combinations of gaze and expression in the stimuli themselves. According to the shared signal hypothesis (Adams & Kleck, 2003, 2005), paired social cues like averted gaze and fear or direct gaze and anger should be processed more efficiently. However, when cues are incongruent (e.g., direct gaze and fear), ambiguity regarding the intentions and feelings of the actor arise and could elicit interactivity. This reasoning is supported by Adams et al. (2003), who found heightened amygdala activity for directly gazing fearful faces and angry faces with averted gaze, a finding which was attributed to the inherent ambiguity of these paired signals. According to appraisal theories (e.g., Sander et al., 2007), certain combinations of gaze and expression should be more self-relevant and hence, processed in a more integrated manner. However, given that typical viewing conditions are lacking social context (e.g., the observer does not know why a particular face is looking at them angrily or looking away fearfully), this may also give rise to ambiguity regarding the intentions of the actor.

The shared-signal and appraisal theories of gaze and expression interactions introduce the notion that certain combinations of gaze and expression may be processed more efficiently than others. This idea may be of particular importance for combinations of gaze and expression that signal threat, in that combinations that unambiguously signal threat (e.g., angry faces with direct gaze and fearful faces with averted gaze) should be processed faster and more accurately than ambiguous combinations. Recent studies suggest that gaze and expression combinations that clearly indicate the presence of threat may be processed reflexively (Adams, Franklin, Kveraga et al., 2011; Adams, Franklin, Nelson et al., 2011). Using fearful and neutral faces with direct and averted gaze, Adams, Franklin, Kveraga and colleagues (2011) demonstrated that when short stimulus durations were employed, amygdala responses were enhanced to fearful faces with averted gaze. This result was also observed for angry faces with direct gaze (Adams, Franklin, Nelson et al., 2011). However, when slower presentations were used, amygdala responses were larger to fearful faces with direct gaze (Adams, Franklin, Kveraga et al., 2011) and angry faces with averted gaze (Adams, Franklin, Nelson et al., 2011). As mentioned previously, Adams and colleagues (Adams, Franklin, Nelson et al., 2011) reported activation of the STS while processing angry faces; however, the locations of these activations varied as a function of stimulus duration, suggesting that STS regions may be differentially recruited by different combinations of gaze and expression in a time-dependent manner. These findings suggest that presentation durations can modulate amygdala and STS responses to fearful and angry gazing faces: faces clearly signaling the presence of threat may be processed reflexively, while more ambiguous combinations of gaze and expression may require more time to process (Adams, Franklin, Kveraga et al., 2011; Adams, Franklin, Nelson et al., 2011).

Ambiguity may also be introduced by the stimuli that are used in a particular task. The use of stimuli portraying less intense facial expressions (e.g., N'Diaye et al., 2009) or more subtle gaze shifts (e.g., Ganel et al., 2005) may promote the use of other facial information in the attempt to resolve a particular facial expression. Motion may also increase the discriminability of gaze and expression changes. For example, using static and dynamic stimuli, Sato et al. (2010) found heightened amygdala activity to dynamic faces displaying expression and gaze changes relative to static faces, and dynamic facial displays are more likely to elicit gaze and expression interactions in gaze cuing studies (e.g., Friesen et al., 2011; Graham et al., 2009; Putman et al., 2006). Relative to static stimuli, featural changes unfold over the course of dynamic stimulus presentations, which may increase the salience and/or discriminability of gaze and expression changes. Neuroimaging studies also differ in how they portray gaze direction. For example, some studies have used changes in head direction to signal the direction of gaze (e.g., Sato et al., 2010, 2004), while others used changes in iris position (e.g., Adams et al., 2003; Hadjikhani et al., 2008; N'Diaye et al., 2009). However, recent research suggests that these differences in the portrayal of gaze direction may have an important role in the emergence of gaze and expression interactions (Ganel, 2011). Specifically, the resolution of gaze direction due to iris displacement may rely on local feature analysis, while head direction may tap into more global processes. Although these issues require further systematic investigation, future research should consider these factors when interpreting their results.

Stimulus duration may also have an important role in the extent to which gaze and expression interact, since brief presentations limit the amount of time that a participant has to scan relevant facial features. For example, Hadjikhani et al. (2008) presented faces for 300 ms and found evidence of interactions in both the amygdala and STS, Straube and colleagues (2010) presented faces for 1000 ms and only found interactions in right STS. Thus, the amount of time available to view faces may alter the discriminability of gaze and expression and increase the likelihood of interactions between these two dimensions. Consistent with this account, Benton (2010) observed that that when fearful and angry faces were presented very rapidly (100 ms), participants were faster to detect emotion in directly gazing angry faces and fearful faces with averted gaze. That these discrepancies may have been due to the role of stimulus duration in evoking gaze and expression interactions was systematically examined using fearful (Adams, Franklin, Kveraga et al., 2011[2]) and angry faces (Adams, Franklin, Nelson et al., 2011). When short stimulus durations were employed, amygdala responses were enhanced to combinations of gaze and expression that clearly signaled threat (Adams, Franklin, Kveraga et al., 2011; Adams, Franklin, Nelson et al., 2011). In contrast, slower presentations were associated with enhanced amygdala responses to more ambiguous combinations of gaze and expression (Adams, Franklin, Kveraga et al., 2011; Adams, Franklin, Nelson et al., 2011). These findings suggest that amygdala responses to fearful and angry gazing faces are moderated by the amount of time allowed to examine the face, with short durations enhancing reflexive processing in the presence of clear threat signals and longer durations promoting more deliberative processing of more ambiguous gaze/expression combinations (Adams, Franklin, Kveraga et al., 2011; Adams, Franklin, Nelson et al., 2011).

It remains to be seen whether the neural pathways subserving these effects are separate parallel pathways (e.g., magnocellular vs. parvocellular) or whether these differential interactions are due to direct or reentrant processing. Event-related potential studies examining these effects and event-related fMRI studies examining the time course of BOLD responses in gaze and expression sensitive areas like the amygdala and STS may help to resolve this issue. In addition, eye-tracking studies using briefly presented, low intensity or otherwise ambiguous stimuli may also help to determine extent to which ambiguity is driving interactions between gaze and expression. Specifically, if stimulus ambiguity is driving these interactions, participants should spend more time scanning relevant facial features and show heightened interactions between gaze and expression. However, if there are no differences in scan paths or scan time but differential interactions are still present, such results would favor a speed-of-processing account.

Task demands also appear to be a factor in the interactivity of gaze and expression. This point is best illustrated by the results of Bindemann et al. (2008), who were able to replicate Adams and Kleck's (2003) observation of enhanced processing for fearful/sad expressions with averted gaze and happy/angry expressions with direct gaze using the same task. However, discrepant results were found with a change in task demands (speeded classification with an increase in the number of response options) that were indicative of a processing advantage for directly gazing faces. Bindemann et al. (2008) speculated that these discrepant results may have been due to the role of eye gaze in the allocation of attention. Given that normal participants have been shown to reflexively orient their attention in response to gazing faces (e.g., Friesen & Kingstone, 1998), the presence of averted gaze may trigger a shift in attention away from the gazing emotional face, interfering with expression processing. This proposition has implications for the discrepant results seen with regard to gaze and expression interactions, as there is considerable variation in the temporal sequencing of gaze and expression changes across experiments. For example, this may explain why studies where the gaze shift preceded the onset of expression changes found evidence of interactivity between gaze and expression information (Friesen et al., 2011; Graham et al., 2009; N'Diaye et al., 2009; Sander et al., 2007), or the primacy of emotional information (Fichtenholtz et al., 2007, 2009), while others using static images that portrayed gaze and expression simultaneously did not (Hietanen & Leppänen, 2003; Straube et al., 2010). However, it is important to note that other studies using static images have found evidence of interactivity between these two stimulus dimensions. In addition, the stimulus sets used in Adams and Kleck (2003) and Bindemann et al. (2008) did not consist of the same faces. Specifically, the faces used in the former study were obtained from a wide variety of sources, whereas the faces used in the latter study were from a widely used, panculturally representative stimulus set. This raises the possibility that differences across the two studies may have been due to differences in the stimulus sets used (i.e., increased stimulus diversity and ambiguity in the Adams & Kleck, 2003 stimulus set). Thus, the possibility that averted gaze may automatically elicit attentional shifts away from the face, interfering with the extraction of emotional information, awaits further study. Eye-tracking studies examining microsaccades to gazing emotional faces may provide some resolution to this issue.

Other possible explanations for discrepant results across experiments include the goals of the observer and, especially in those experiments involving gaze cuing, the amount of contextual information provided in the task. While some experiments require that the participant identify or rate the intensity of gaze or expression, others explicitly require shifts in attention in order to successfully perform the task. The temporal sequencing of gaze and expression changes may affect the extent to which interactions occur. However, in gaze cuing tasks, these attentional shifts are required in order to detect or identify subsequent targets. This task demand may lead to faster detection of gaze when expression and gaze shifts are presented simultaneously, and changes in the allocation of attention that interfere with the extraction of expression information. In comparison, tasks requiring the identification of emotions or gaze direction without requiring a change in the location of visual attention may be more likely to show evidence of interactivity of these two stimulus dimensions. Differences in the response requirements of experiments may also affect the observed results. For example, in one experiment, Bindemann et al. (2008) used a four-choice paradigm, which slowed reaction times and increased error rates. In this experiment, there was also an advantage for faces with direct gaze. The increase in the number of response options

[2] This study was a collaboration between Adams and Hadjikhani that was motivated by the discrepant results across studies using varied stimulus durations.

available to participants may have increased the difficulty of the task without increasing perceptual demands per se, leading to the observed results. The exact role of response requirements in studies examining gaze and expression interactions awaits further study.

Finally, in many of the cuing studies yielding discrepant results, targets were emotionally neutral. However, with the introduction of emotionally relevant targets, more consistent interactions between gaze and expression have been observed (e.g., Bayliss, di Pelligrino, & Tipper, 2005; Bayliss, Frischen et al., 2007; Fichtenholtz et al., 2007; Friesen et al., 2011; Pecchinenda et al., 2008). This suggests that for expression processing to be fully engaged in gaze cuing studies, it might be necessary to present targets that would logically elicit emotional expressions in a gazing face. Using a novel oculomotor visual search task based on a standard gaze cuing paradigm, Kuhn and Tipples (2011) reported an advantage for gazing fearful faces for threatening targets that disappeared for pleasant targets. Together, these studies suggest that contextual factors such as the use of meaningful targets and task demands may be particularly important in eliciting interactions between gaze and expression. Given that social communication is situated in real-world contexts that involve a variety of cues beyond that of gaze and expression (e.g., vocalizations, body-postures and situational contexts), it is reasonable to expect that the integration of gaze and expression is critically dependent upon the specific situations in which they occur (see Kingstone, 2009), which includes the complexity of the stimuli, the expectations and demands on the observer.

5.3. Future directions

A fruitful area of future inquiry is to examine individual differences (e.g., empathy, self-esteem, anxiety) in gaze and expression integration. Given that personality variables like trait fearfulness or anxiety can influence face processing, such as reflexive orienting to gaze direction (e.g., Tipples, 2006; Wilkowski, Robinson, & Friesen, 2009), then personality variables may affect how information from faces is processed/integrated by different individuals, especially those with a history of depression or anxiety disorders (Bradley et al., 2000; Mogg et al., 2004). Individual differences in the ability to extract facial information about gaze and expression are particularly germane to the notion of ambiguity and its role in the interactivity of these two dimensions. Differences in sensitivity to either or both of these dimensions means that what is ambiguous to some might not be to others. For example, Adams and Franklin (2009) found that individuals that were slower to make responses about gaze direction also showed stronger interaction effects. Given that sensitivity to facial expression and gaze direction do vary across individuals within normal populations (e.g., see Bayliss, de Pelligrino, & Tipper, 2005; Montagne, Kessels, Frigerio, de Haan, & Perrett, 2005 for discussions about gender differences in sensitivity to gaze and expression) and across development (e.g., see Thomas, Debellis, Graham, & LaBar, 2007 for differences in sensitivity to facial expression across childhood and adolescence), these differences in sensitivity may yield important insights into the nature of gaze and expression interactions. For example, sex hormones may have a role in moderating gaze and expression interactions. Conway et al. (2007) examined women at two different stages of the menstrual cycle and found that women were more likely to perceive fearful and disgusted expressions (but not happy expressions) with averted gaze as more intense than those with direct gaze when their progesterone levels were high. A better understanding of the individual difference and situational factors that help to determine differential sensitivity to these dimensions should advance conceptual knowledge and clarify the existing literature.

Another interesting avenue for future research is the influence of cultural differences in interactivity. Given that studies on this topic are conducted across a wide variety of cultural settings and populations, cultural differences may play an important role in the nature of gaze and expression interactions. For example, using a reverse correlation technique, Jack, Caldara, and Schyns (2011) presented a neutral face overlaid with different patterns of white noise to Caucasian and Chinese participants and had them categorize the faces by facial expression. Relative to Caucasians, Chinese participants showed a preference for information in the eye region, perceived gaze direction in particular. Furthermore, gaze direction was used by Chinese participants to resolve a wider range of facial expressions (fear, anger, sadness, surprise and disgust) than Caucasians (sadness). Adams, Franklin, Nelson et al. (2010) and Adams, Franklin, Rule et al. (2010) examined the effect of culture (Asian vs. Caucasian) on gaze and expression interactions in response to fearful faces. Significant interactions between participant culture and own- vs. other-race faces were observed in several brain regions also implicated in face processing, including the fusiform gyri, insula and amygdala, as well as in dorsolateral and ventrolateral prefrontal cortices. Activity in these areas increased in response to other-race faces with directly gazing fearful faces, in particular, in bilateral amygdalae. However, amygdala responses were enhanced to own-race fearful faces with averted gaze in US participants, replicating Hadjikhani et al. (2008). In contrast, Japanese participants did not show such an interaction: amygdala activations to own-race fearful faces did not vary as a function of gaze, presumably due to the fact that direct gaze may be construed as threatening in this culture (Adams, Franklin, Nelson et al., 2010; Adams, Franklin, Rule et al., 2010; but see Matsumoto & Ekman, 1989 for evidence suggesting that Japanese participants are more likely to perceive fear in FACS-coded faces as surprise). Cultural studies must also take into consideration racial differences in the physiognomy of facial features, such as eye aperture, that may affect the resolvability of gaze and affect cues. Although further research is necessary, cultural differences may account for some discrepancies in the literature.

Another area for further scrutiny is the combined role of gaze and expression in signaling complex emotions, like thoughtfulness, embarrassment, contempt, shame, boredom, arrogance and flirtation (to name a few), where information about the actor's internal state is conveyed through both facial expression and eye gaze (Adolphs, Baron-Cohen, & Tranel, 2002; Baron-Cohen, Wheelwright, & Joliffe, 1997). As such, successful decoding of these emotions should require the integration of gaze and expression to a greater extent than the decoding of basic emotions like surprise, fear, disgust, anger, happiness and sadness. Studies examining the perception of complex emotions have demonstrated the importance of the eye region in inferring these mental states and deficits in the ability to decode these emotions in autistic individuals (Baron-Cohen et al., 1997). A subsequent fMRI study by Baron-Cohen et al. (1999) showed that making these more complex social judgments about faces resulted in activations of the amygdala and superior temporal gyrus in control participants, but not autistic individuals. The role of the amygdala in decoding complex emotions is underscored by the findings of Adolphs et al. (2002), who observed impaired recognition of these emotions in amygdala-damaged patients relative to brain-damaged controls. These deficits were more marked than those observed for basic emotional expressions, and when judgments were made from information restricted to the eye regions (Adolphs et al., 2002). The perception of complex social emotions should maximize the integration of gaze and expression, and incorporating these stimuli into the systematic investigation and comparison of various theories and accounts of gaze and expression interactions may help to reconcile the inconsistencies observed with basic emotional expressions.

An understanding of gaze and emotion processing in healthy adults provides a basis for delineating how these processes might be disrupted by development, disease or injury. Because insights into mental chronometry have relevance for distinguishing and understanding affective disorders (Davidson, 1998), future research should strive to better characterize the development of gaze and expression interactions. For example, although there is evidence that gaze and happy facial expressions are not processed in an integral manner until 12 months of age (Phillips et al., 2002), more research is necessary to determine if this results generalizes across a variety of facial expressions, and to better characterize the developmental trajectory of gaze and expression interactions and how they might be affected by socioaffective disorders and autism. A recent study by Akechi et al. (2009), based on Adams and Kleck (2003), suggests that previously reported gaze and expression interactions to fearful and angry faces may be absent in children with autism. While typically developing children showed enhanced processing of directly gazing angry faces and fearful faces with averted gaze, autistic children did not. These results are significant for two reasons. First, they demonstrate that in typically developing children (9–14 years old), gaze and expression interactions are similar to those found in adults. Second, they suggest that the ability to spontaneously integrate these two facial dimensions is impaired in autism, which was speculatively attributed to either amygdala or prefrontal function (Akechi et al., 2009). Some studies have shown evidence of gaze and expression interactions in the cerebellum (e.g., Adams, Frankin, Kveraga et al., 2011; Sato et al., 2010, 2004), which has also been implicated in implicit processing of facial expression (Critchley et al., 2000). The role of the cerebellum in social processing is currently not well understood; however, developmental cerebellar abnormalities associated with autism (Courchesne, Yeung Courchesne, Press, Hesselink, & Jernigan, 1988) and acquired cerebellar damage (Schmahman & Sherman, 1998) have been associated with impaired social function. Further research is necessary to elucidate the role of this structure in socio-emotional processing.

In summary, this review of the extant literature provides new evidence for the effects of gaze direction and emotional expression on multiple neural processes, helping to characterize the temporal mechanisms of shared attention and social referencing and the conditions under which these two facial dimensions interact to influence social cognition. Future studies in this area should further examine the following issues: investigate the task sensitivity of gaze and expression interactions, use eye-tracking and ERP methods to resolve interdependence of processing in the Garner task, develop designs that pit theoretical arguments against each other, move toward dynamic, ecologically valid and socially relevant paradigms, investigate individual and cultural differences, and extend the research into clinical populations. Overall, recent behavioral and neuroscientific evidence suggests that within the dynamic or viewer-centered stream, changes in eye gaze and emotional expression can have independent effects on face judgments and covert shifts of visuospatial attention. These effects may be at least partially segregated during initial visual processing, but are subsequently integrated in limbic regions such as the amygdala or via reentrant visual processing volleys to STS that may be susceptible to top-down processes. If it is indeed the case that early visual processing, including the integration of different streams of information in the face, can be affected by top-down processes, deficits in social processing may be remediated by the use of controlled strategies and intentional therapies. Lessons learned from the study of gaze-expression interactions could inform neurocognitive theories of other socioemotional communication phenomena, including the integration of facial and vocal affect or expression and gestures/body postures. Such efforts will help delineate the complex mechanisms that guide our seamless and nuanced social exchanges and identify how these communication channels break down in affective disorders.

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