

The eyes as windows into other minds: An integrative perspective

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Abstract

Eyes have been shown to play a key role during human social interactions. However, to date, there is no comprehensive model that integrates across disciplines and provides a framework that can account for uniquely human forms of responding to eye cues. In this review, I will present a framework that brings together work on the phylogenetic, ontogenetic and neural bases of perceiving and responding to eyes. Specifically, I will argue for a two-process model according to which a first process ensures privileged attention to information encoded in the eyes and is important for the detection of other minds, and a second process permits for the decoding of information contained in the eyes concerning another person's emotional and mental states. These processes are to some degree unique to humans, emerge during different times in infant development, can be mapped onto distinct but interconnected brain regions, and likely serve critical functions in facilitating cooperative interactions in humans. I will also present evidence to show that oxytocin is a key modulator of sensitive responding to eye cues. Viewing eyes as windows into other minds can therefore be considered a hallmark feature of human social functioning deeply rooted in our biology.

Keywords: Social Cognition, Development, Neuroscience, Comparative Psychology

Introduction

Eyes are sometimes metaphorically referred to as windows to our souls. Indeed, there has been much work to investigate the psychology of perceiving and responding to eye cues. This research unanimously supports the notion that much information about other minds can be gleaned from the eyes, and that this information provides a vital basis for initiating, maintaining and regulating social interactions among humans. Although what exactly can be read from the eyes about other minds might be limited, psychological research on this question speaks against the argument (first made by philosophers in the skeptical tradition) that the presence and contents of other minds cannot be directly observed – an issue also referred to as the problem of other minds. The argument put forward in this paper is that eyes provide a bridge between self and other, and that human responding to eyes can be seen as an adaptive solution to problems posed by the difficulty of making inferences about other minds. In particular, I will argue that responding to eyes serves three key functions in humans: (1) detecting the presence of other minds, (2) inferring the content of other minds, and (3) fostering collaboration with other minds. In combination, these functions make up a powerful tool for navigating our social environments.

There is a body of prior work that stresses the role of eyes in human cognition from phylogenetic, ontogenetic, and neuroscientific perspectives (Baron-Cohen, 1994; Emery, 2000; Kobayashi & Kohshima, 1997, 2001; Pelphrey & Morris, 2006; Tomasello, Hare, Lehmann, & Call, 2007). For example, Tomasello and colleagues (2007) found that in human infants, but not in chimpanzees, gaze following is driven by eye gaze cues and conclude that human eyes evolved to make it easier for others to follow gaze and thereby facilitate cooperative interaction. Relatedly, Baron-Cohen (1994) has argued that human infants possess a module termed the *Eye Direction Detector*

that enables them to detect the presence of eyes and also represents eye gaze and what others have visual access to. At the neural level, specific brain processes have been identified that are engaged when viewing eyes and responding to eye cues in human adults (Kampe, Frith, & Frith, 2003; Pelphrey & Morris, 2006; Pelphrey, Viola, & McCarthy, 2004). Importantly, the brain processes engaged when dealing with information from eyes are similar to when thinking about other people's mental states such as intentions and beliefs (Frith & Frith, 2006; Kampe et al., 2003; Pelphrey & Morris, 2006). What is missing, however, is a single framework that attempts to integrate across these multiple levels of analysis (Tinbergen, 1963) and thereby specifies the role that eyes play in human social cognition. The goal of the current review therefore is to integrate the available evidence from comparative, developmental, and neural investigations into a novel and comprehensive framework that informs our understanding of how humans respond to eye cues and what adaptive function this may serve. In the following, I will in turn review the existing evidence on the phylogenetic, ontogenetic, and neural basis of perceiving and responding to eyes. In addition, I will also present evidence to show that oxytocin can be considered a key neurochemical modulator of sensitive responding to eye cues. This approach will allow us to shed light onto the evolutionary and developmental pathways that have sculpted the human brain to treat eyes as a window into other minds. Because the current review spans across multiple levels of analysis to illuminate social eye cue processing in humans, it is important to acknowledge that it is beyond the scope of this review to provide a comprehensive review of all aspects of sensitive responding to eyes (for more details, see Nasiopoulos, Risko, & Kingstone, 2015; Pfeiffer, Vogeley, & Schilbach, 2013; Schilbach, 2015; Schilbach et al., 2013).

Phylogeny

From a comparative perspective, it is critical to determine whether the human eye possesses any features that set them apart from the eyes of other primates. Based on a comparison with nearly half of all primate species (88 species), the human eye has been shown to be morphologically unique (Kobayashi & Kohshima, 1997). In particular, when compared to other primates, humans not only show the largest amount of exposed sclera and greatest horizontal elongation of the eye outline, but they are also the only species with white sclera (Kobayashi & Kohshima, 1997, 2001; also see Mayhew & Gomez, 2015, for recent work with gorillas arguing that the horizontal elongation rather than sclera color distinguishes humans from great ape eyes). Importantly, it has been shown that these morphological parameters, identified to be specifically developed in humans, positively correlate with social complexity as reflected in group size and neo-cortex ratio across 30 living primate species (Kobayashi & Hashiya, 2011). The comparative analysis of eye morphology has led to the proposal that these unique characteristics of the human eye are of adaptive value as they extend the visual scanning in the horizontal direction for the individual and facilitate the detection of eye cues and especially gaze direction from other individuals (Kobayashi & Kohshima, 2001). The former might be advantageous to humans as a large and terrestrial primate species, where horizontal eye movements are more important and effective than whole body or head movements when scanning the environment. The latter is argued to have been instrumental in the evolution of contact-free social ‘grooming’ functions of eye gaze (Kobayashi & Hashiya, 2011) and is thought to be particularly beneficial to humans as a highly cooperative species that heavily relies upon communication when coordinating actions. This emphasis on the advantages of eye-based social communication in the service of cooperative

interactions based on the morphological differences highlighted above, has culminated in the formulation of the ‘cooperative eye hypothesis’ (Tomasello et al., 2007).

With respect to the proposed unique role that eyes serve in human cooperative interactions, is there any evidence to suggest that humans pay special attention to the eyes and utilize information from the eyes more than other primates? When compared to chimpanzees (our closest living primate relatives), humans show a greater focus on the eye region when scanning faces (Kano & Tomonaga, 2010). This finding from eye-tracking work indicates that in humans, eyes are particularly powerful in grabbing attention. Similar evidence for prolonged eye viewing in humans also exists when comparing human face scanning patterns to other great apes such as gorillas and orangutans (Kano, Call, & Tomonaga, 2012). Furthermore, in contrast to other great apes (chimpanzees, bonobos, and gorillas), human infants almost exclusively rely on eye direction when following gaze, whereas other great apes relied more on head direction (Tomasello et al., 2007). Together findings from these comparative studies suggest that humans, when compared to other great apes, attend and respond to eyes in unique ways. Note that this is also not to say that other primates do not also respond sensitively to conspecifics’ eyes and their gaze (see Emery, 2000), but rather to stress that humans seek out, scrutinize, and utilize information from the eyes differently than other great apes.

Recently, using eye-tracking it has also been shown that, when comparing between humans’ two closest primate living relatives- bonobos and chimpanzees- bonobos devoted more attention to the eye region when scanning faces than chimpanzees (Kano, Hirata, & Call, 2015). This is taken to suggest that bonobos are more similar to humans as far as their tendency to orient and attend to the eyes is concerned, although, in this study, humans and bonobos were not directly compared

to each other. Furthermore, as mentioned before, even though bonobos might spend more time looking at the eyes they still do not seem to use information from the eyes to inform their gaze following behavior (see Tomasello et al., 2007). In this context, it is also important to mention that domestic dogs exhibit an attentional bias towards the eye region when scanning conspecific and human faces (Somppi et al., 2016). These findings with bonobos and dogs point towards interesting similarities with humans, which need to be taken into consideration in addition to the dissimilarities between chimpanzees and humans. They further indicate the need to more systematically map similarities and differences in eye processing across species (see MacLean et al., 2011) in order to arrive at a better understanding of the evolution of the sensitivity to eyes.

Another critical question to address here is whether human-specific responding to eyes goes beyond increased attention and gaze following and especially whether, as stipulated in the ‘cooperative eye hypothesis’ (Tomasello et al., 2007), human eyes in fact facilitate cooperation among humans. In support of this notion, there is evidence from a mounting number of studies using economic games to suggest that subtle eye cues have an effect on cooperation (Bateson, Nettle, & Roberts, 2006; Burnham & Hare, 2007; Ernest-Jones, Nettle, & Bateson, 2011; Haley & Fessler, 2005; Nettle, Harper, et al., 2012; Nettle, Nott, & Bateson, 2012). Specifically, both in laboratory and real-life contexts, the presence of eyes has been shown to increase cooperative behavior in humans (Bateson et al., 2006; Burnham & Hare, 2007; Ernest-Jones et al., 2011; Haley & Fessler, 2005). For example, human adults put nearly three times as much money into an honesty box used to collect money for drinks when a pair of eyes were placed above the honesty box than when a control image (flowers) was placed in the same location (Bateson et al., 2006). Recently, it has been shown that, in contrast to what is known about humans, chimpanzees do not

change their behavior depending on the presence of eye cues (Nettle, Cronin, & Bateson, 2013). The observed sensitivity to eye cues in humans and its effects on cooperative behavior is thought to emerge out of reputational concerns related to being watched (Haley & Fessler, 2005).

In summary, there is compelling evidence from comparative psychology to suggest that human eyes are not only morphologically unique among primates, but also that humans, compared to other great apes, possess a unique sensitivity to information from the eyes. Namely, human responding to eyes is characterized by increased attention to and utilization of eye cues. This enhanced sensitivity to eyes likely functions in the service of fostering human cooperative behavior. This view through the lens of comparative psychology provides insights into what can be considered uniquely human about responding to eyes. Now that human-unique patterns of responding to eyes have been identified through the comparative work reviewed, in order to achieve a fuller understanding how of this sensitivity comes about in humans, it is important to elucidate its ontogenetic origins.

Ontogeny

The sensitivity to eyes emerges early in human development. From birth, newborn infants show a preference for faces, despite their poor visual acuity (Goren, Sarty, & Wu, 1975; Johnson, 2005; Johnson, Dziurawiec, Ellis, & Morton, 1991). There is some debate as to what the exact mechanism is that underlies newborn infants' face preference, but one computational mechanism that has been shown to produce newborn-face like preferences in modeling work is based on binocular integration, which results in heightened salience of the eye region (see Wilkinson, Paikan, Gredebäck, Rea, & Metta, 2014). Behavioral experiments show that

preferential orienting to faces seen in newborns at close range (30 cm viewing distance) is likely driven by information from the eyes (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000; Farroni, Csibra, Simion, & Johnson, 2002; Farroni et al., 2005). For example, newborns have been shown to prefer to look at faces with their eyes open when compared to faces with their eyes closed (Batki et al., 2000). Moreover, newborns exhibit a visual preference for the face only when they view pictures of faces that contain naturally appearing eyes (black iris and white sclera), but not when they view contrast-inverted control faces (with a white iris and black sclera) (Farroni et al., 2005). While such human-specific features of the eyes contribute to face preferences seen in newborn infants, there also is recent evidence to suggest that human eyes alone are not sufficient to produce face preferences in newborns. Specifically, 3-month-old-infants, but not newborns, show a preference for nonhuman primate faces with human eyes when compared to nonhuman primate faces with their natural eyes (Dupierrix et al., 2014). This suggests that a preference for human eyes without other human facial features develops over the course of the first few months after birth.

Soon after birth infants are also able to pick up on directional eye gaze cues as evident in their preference for direct gaze (eye contact) (Farroni et al., 2002), and a rudimentary form of gaze following is found in newborns (Farroni, Massaccesi, Pividori, & Johnson, 2004). Around one month of age, but not younger, agitated infants have been shown to be most effectively calmed by sucrose administration accompanied by eye contact, suggesting the emergence of reliance on eye cues during social interactions (Zeifman, Delaney, & Blass, 1996). Furthermore, around 7 weeks of age infants have been shown to increase fixations on the eye region when scanning faces (Haith, Bergman, & Moore, 1977). This suggests that the basis for the human

capacity to attend to and utilize information from the eyes develops very early in ontogeny.

While a basic sensitivity to eyes is present in newborns and may serve as an important foundation for later developing eye reading skills, infants' responses to eye cues develop and become more sophisticated over the course of infancy. This developmental trend becomes particularly apparent when looking at infants' gaze following responses. By around 2 to 3 months of age, gaze following responses during live social interaction require special triggering conditions, including constant infant-directed speech and target objects that are very close to the presenter's face (D'Entremont, Hains, & Muir, 1997; Scaife & Bruner, 1975). By about 6 months, infants follow gaze to more distant targets (Butterworth & Itakura, 2000; Butterworth & Jarrett, 1991), and gaze following responses to a target become reliable between 7 and 9 months of age (Flom & Pick, 2005; Woodward, 2003). However, at 12 months, appropriate gaze following responses are still fragile when several potential targets are available and it is not until the second year of life that infants' gaze following becomes more robust under challenging circumstances (Butterworth, 1991; Deák, Flom, & Pick, 2000; Flom, Deák, Phill, & Pick, 2004). This is because young infants usually direct their gaze to the first object on the gaze-cued side rather than identifying the exact object the person is looking at (Morales, Mundy, & Rojas, 1998), and they need additional referential cues such as pointing in order to successfully select the correct object to direct their gaze to (Deák et al., 2000; Flom et al., 2004). Furthermore, 9-month-old infants reflexively follow the head turn of a person even when their eyes are closed, whereas 10-month-old infants refrain from gaze following in this context (Brooks & Meltzoff, 2002). Along these lines, only by around 12 months of age do infants view eye gaze as an intentional action as seen in their ability to encode the

relationship between a person's eye gaze and a target object as goal-directed (Woodward, 2003). However, until the age of 14 months, infants follow blindfolded people's head turns (Brooks & Meltzoff, 2002), whereas after this age, infants start to take into account whether the other has visual access to the target object (Caron, Keil, Dayton, & Butler, 2002; Dunphy-Lelii & Wellman, 2004) and to correctly integrate information from head and eye direction (Caron, Butler, & Brooks, 2002). Taken together, these findings from infant gaze following studies suggest that during infancy the ability to use eye gaze becomes more sophisticated (flexible and accurate) not only in terms of discerning a person's eye gaze direction but also in viewing another person's eye gaze as intentional and goal-directed. More generally, this development is thought to serve the function of enabling infants to share attention with others during joint activities that underpin human cooperation (Tomasello & Carpenter, 2007; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012).

Another kind of information that can be gleaned from the eyes is the detection of emotional and mental states from the eye region, which has been extensively studied in adults and children but has thus far not received much attention in infants (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Franco et al., 2014). However, there is some evidence to suggest that infants engage processes that are indicative of the detection of such information from the eyes. For example, when attending to eye cues, 4-month-old infants have been shown to recruit brain regions that in adults are associated with 'mind reading' or 'theory of mind' (Grossmann, 2013; Grossmann & Johnson, 2010; Grossmann et al., 2008; Grossmann, Lloyd-Fox, & Johnson, 2013). In particular, similar to adults (Kampe et al., 2003; Pelphrey et al., 2004), viewing direct gaze activates medial prefrontal cortex and posterior superior

temporal cortex in 4-month-old infants (Grossmann et al., 2008). Medial prefrontal regions have also been found to be involved during social interactions in which 5-month-old infants followed another person's eye gaze (Grossmann & Johnson, 2010) or the person followed the infants' eye gaze (Grossmann et al., 2013). Similar to adults (Whalen et al., 2004), 7-month-old infants have been shown to detect fear solely on the basis of eye whites/sclerae using event-related brain potentials (ERPs) (Jessen & Grossmann, 2014). In this study, infants' detection of fear was specific to the human sclera and not seen in response to polarity-inverted eyes (white iris, black sclera). Noticeably, while suggestive, these findings from the brain imaging studies with infants do not provide direct evidence that infants indeed engage in emotional or mental state attribution during these social encounters.

More evidence for the possibility that eyes play an important role in infants' detection of mental states comes from work on infants' social evaluations (Hamlin, Wynn, & Bloom, 2007). Specifically, this work has shown that infants prefer to interact with (touch) an individual that helped another individual to one that hindered another individual in reaching its goal (climbing the top of a hill). In these experiments, wooden colored geometric shapes (circle, square, and triangle) were used as characters to portray the helping and hindering actions. Important for the current context, these effects on infants' social evaluations reflected in their preferential touching were only seen when these characters had eyes but not when they performed the same actions without eyes. Moreover, a recent study showed that only when the character climbing the hill was gazing toward his goal (top of the hill) did infants show a preference for helping over hindering characters (Hamlin, 2015). Together, these findings provide evidence for the notion that eyes are involved in detecting whether or not others are performing intentional actions. Interestingly, these findings further

suggest that eye cues help infants to distinguish between prosocial and antisocial individuals, an ability that is presumably of great value for regulating cooperative behavior. Moreover, later in development, social eye cues have been shown to help children coordinate their behavior and decision-making in cooperative tasks. Namely, 4-year-old children use mutual gaze as a cue to coordinate their actions for cooperative purposes in a 'stag hunt' game (see Wyman, Rakoczy, & Tomasello, 2013).

In summary, there is mounting evidence from developmental psychology to suggest that already newborns are sensitive to human eyes and that the ability to attend to and utilize eye cues develops rapidly over the course of infancy. Specifically, we have seen that infants not only become avid readers of eye cues as evident in their responses to directional, emotional and intentional information conveyed by the eyes, but also that the presence of eyes can impact infants' evaluations of and engagement with others. This view through the lens of developmental psychology provides insights into the ontogenetic origins of what can be considered uniquely human responding to eyes. Together with the phylogenetic perspective outlined above, a coherent picture begins to emerge that identifies eyes as playing a key role in human social functioning.

Brain

Given what we discussed with respect to the phylogenetic and ontogenetic origins of responding to eye cues, the question emerges: What brain processes underpin this specific sensitivity to eyes in humans? One key brain region that has been implicated in sensitive responding to eyes is the amygdala. In particular, there is evidence from a patient with bilateral amygdala damage who shows a lack of spontaneous fixations of the eye region during free viewing of faces (Adolphs et al.,

2005). This lack of fixations of the eye region during processing faces likely accounts for a selectively impaired recognition of fear from faces (when compared to other basic emotions displayed in the face) also found in this patient with amygdala damage. Fearful faces are mainly characterized by and identified through the widely open eyes with large visible sclera (Adolphs et al., 2005). Intriguingly, when this patient with amygdala damage was explicitly asked to pay attention to the eyes, her recognition of fear in faces was restored. This suggests that amygdala damage does not directly result in an impairment of fear recognition but rather impacts fear recognition through a failure to scan the face for eye cues (see Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009, for evidence regarding this notion). That the amygdala plays an important role in processing eye cues has also been shown in functional magnetic resonance imaging (fMRI) studies in healthy adults (but see Boubela et al., 2015, for evidence that amygdala activation measured with fMRI might be confounded by stimulus-correlated signal fluctuations by nearby veins draining distant brain regions). For example, the amygdala is involved in the detection of widely open (fearful) eyes (Whalen et al., 2004). Specifically, in this study, amygdala involvement was seen in response to fearful eye whites, but not to polarity-inverted control stimuli or happy eye whites, and it occurred even in the absence of conscious perception. Taken together, these findings suggest that the amygdala is a key brain structure implicated in spontaneously directing attention to eye cues and in the automatic detection of eye cues (specifically fear).

In addition to the basic amygdala-based orienting to and detection of eye cues, the more complex analysis of eye cues also involves cortical brain regions such as the posterior superior temporal sulcus (pSTS) and the medial prefrontal cortex (mPFC) (Baron-Cohen et al., 1999; Kampe et al., 2003; Pelphrey & Morris, 2006). These

brain regions have been generally implicated in mental state reasoning in adults (Frith & Frith, 1999, 2006, 2007), suggesting that responding to eye cues engages mind reading processes. More evidence for this notion comes from behavioral work showing that eyes are the critical features of a face that guide us in perceiving others as having minds (Looser & Wheatley, 2010). With respect to the cortical brain regions involved and most relevant for the current context, pSTS and mPFC have been associated with the detection of a person's goals and communicative intentions from eye cues (Kampe et al., 2003; Pelphrey & Morris, 2006). For example, pSTS, as a region involved in biological motion processing (Allison, Puce, & McCarthy, 2000), is sensitive to the goal of a person's eye gaze insofar as it distinguishes between object congruent and incongruent eye gaze shifts and mutual and averted gaze (Pelphrey & Morris, 2006). Furthermore, mPFC, as a region involved in mental state reasoning (Amodio & Frith, 2006), is sensitive to eye gaze cues (mutual gaze) and vocal cues (calling of the first name) that indexed the intention to communicate (Kampe et al., 2003). These findings suggest that viewing eye cues results in cortical activation patterns that indicate the involvement of mind reading (theory of mind) processes.

With respect to the brain processes involved in responding to eye cues, it is important to mention that in addition to the brain processes discussed above reward-related brain regions such as the ventral striatum have been implicated in eye gaze-based social interactions in human adults (Pfeiffer et al., 2014; Schilbach et al., 2010). Specifically, recent neuroimaging work using real-time interactive paradigms has shown that the experience of social engagement with a virtual human agent based on reciprocal eye gaze towards specific objects is associated with increased activity in the ventral striatum (Pfeiffer et al., 2014; Schilbach et al., 2010). This is taken to suggest that experiencing these kinds of eye gaze interactions is rewarding, which in turn

might serve an important function in maintaining and motivating cooperative gaze behavior. Importantly, ventral striatal activity occurred regardless of whether or not the participant was explicitly instructed to believe that the social partner was cooperative (Pfeiffer et al., 2014). This suggests that the experience of social engagement that emerges out of the social interaction (bottom-up), but not the explicit attribution of intentional cooperative motives (top-down), drives recruitment of reward-related neural circuits. While due to methodological limitations ventral striatal activity has not been assessed in infants, it is noteworthy that infants were found to show greater left prefrontal activation when a social partner followed their gaze (Grossmann et al., 2013), which has been argued to reflect appetitive motivational tendencies related to approach (Davidson & Fox, 1982; Fox, 1991; Harmon-Jones, 2003). This raises the possibility that in both infants and adults, there exist motivational processes that help guide gaze-based social interactions.

In summary, there is considerable evidence from social neuroscience to suggest that there is a well-attuned network of brain regions that underpins sensitive responding to eye cues. Specifically, we have seen that while subcortical structures such as the amygdala are involved in orienting to eye cues, cortical regions such as the pSTS and mPFC allow for the analysis of eye cues with respect to the associated mental states. Furthermore, brain processes associated with reward appear to play a role in motivating (reciprocal) social eye gaze behavior and may reinforce tendencies to interact with others through using gaze cooperatively. This view through the lens of neuroscience provides information regarding the brain basis of responding to eyes in humans. These brain level findings from adults provide critical additional information to the ontogenetic and phylogenetic perspectives outlined above, as they allow us to

describe the brain mechanisms that have been shaped by evolutionary and ontogenetic forces.

Oxytocin

Oxytocin is a neurohormone (neurotransmitter and hormone) found in mammals that is produced by the hypothalamus and stored and secreted by the posterior pituitary gland (Meyer-Lindenberg, Domes, Kirsch, & Heinrichs, 2011). As a neurohormone, oxytocin has been identified as playing a major role in facilitating birth, lactation, and maternal behaviors, but also has been shown to impact and more generally regulate social behaviors in humans and other mammals (Burkett, Andari, Johnson, Curry, de Waal, & Young, 2016; Carter, 2014; Meyer-Lindenberg et al., 2011). Recently, on the basis of extensive research on the effects of oxytocin, it has been proposed that oxytocin is critically involved in the evolution of the high levels of sociality characteristic of humans as an ultra cooperative species (Carter, 2014). For example, there is evidence to show that oxytocin when administered intra-nasally increases trust and altruism in humans (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Zak, Stanton, & Ahmadi, 2007). Critically, intranasal administration of oxytocin has been shown to result in elevated levels of oxytocin in blood and cerebrospinal fluid in humans (Striepens et al., 2013). With respect to the role that oxytocin plays for social behavior it should be noted that recent work paints a more complicated and nuanced picture, suggesting that rather than generally increasing prosociality in humans, oxytocin may favor prosocial tendencies towards in-group over out-group members (De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2011; Shalvi & De Dreu, 2014) and might indeed play a more complex role in regulating affiliative behaviors (Ebitz & Platt, 2014).

Importantly with respect to the current topic, it has been shown that the administration of oxytocin results in increased fixations to the eyes when viewing faces (Auyeung et al., 2015; Guastella, Mitchell, & Dadds, 2008). Oxytocin administration does not only increase fixations on the eye region but also significantly enhances the recognition of emotional and mental states from eye cues (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007). In this study, oxytocin administration was associated with an improved performance in the ‘Reading the Mind in the Eye Task’ (see Baron-Cohen et al., 2001). At the brain level, there is recent work to suggest that the amygdala plays a mediating role in driving these effects of oxytocin on eye cue detection (Gamer, Zurowski, & Büchel, 2010). Specifically, the results from this study show that oxytocin affects activity within the posterior amygdala (and its functional connectivity with the superior colliculus) associated with increased gazing at the eye region, whereas differential activity within the anterior amygdala in response to oxytocin distinguishes between different emotional states conveyed by a face (reduction to fear and increase to happiness). In another study, oxytocin administration resulted in a reduction of amygdala activity in response to emotional facial expressions of fear and anger and in a decrease of the connectivity between the amygdala and brainstem regions involved in the display of fearful behavior (Kirsch et al., 2005). This is taken to reflect reduced levels of anxiety during social encounters, which might also relate to the increased levels of trust shown after oxytocin administration (Kosfeld et al., 2005). Together these findings from oxytocin administration studies in human adults suggest that oxytocin promotes sensitive responding to eye cues, presumably as a result of regulating amygdala activity during face viewing.

From a comparative perspective, it is important to mention that there is recent work to suggest that oxytocin administration increases fixations on the eye region, but not overall attention to the face, in rhesus monkeys (Dal Monte, Noble, Costa, & Averbeck, 2014). This specific orienting bias to the eyes (relative to the mouth) occurred in rhesus monkeys while freely viewing conspecific faces after oxytocin administration. This pattern found in rhesus monkeys is particularly striking given that in many monkey species looking a conspecific in the eye (direct eye contact) often elicits aggressive displays and attacks (Kobayashi & Kohshima, 1997, 2001). In this context, it is also important to acknowledge recent work with domestic dogs showing that (a) gazing behavior from dogs increases oxytocin levels in the owner, and (b) intranasally administered oxytocin increases dogs' gazing at their owners, which was in turn associated with enhanced oxytocin levels in the owners (Nagasawa et al., 2015). This suggests that oxytocin-mediated mutual gazing patterns exist across species in closely affiliated human-dog bonds. It should be noted that, in this study, dogs' gazing behavior was not precisely monitored using eye-tracking, and it is therefore not possible to evaluate to which extent gazing reflects looking at the eyes of the owner. However, another study mentioned above, shows that dogs preferentially look at the eye region when scanning human faces (see Somppi et al., 2016), which indicates that looking at the eyes (mutual eye gaze) may also play a role in Nagasawa et al.'s (2015) study.

One possibility is that rather than directly promoting looking to the eye region, oxytocin may instead decrease anxiety and aggression, which in turn results in an increase in fixations on the eyes. In other words, increased attention to the eye region might be an indirect outcome of reduced anxiety in response to oxytocin during social encounters. This view is in line with what is known regarding the anxiolytic and trust

promoting effects of oxytocin in humans mentioned above, and it also concurs with conceptual proposals stipulating that oxytocin serves a dual function during social encounters. Namely, oxytocin is thought to increase approach while simultaneously reducing withdrawal during human social encounters (Kemp & Guastella, 2011). This proposal regarding the role of oxytocin in human social functioning converges with existing evolutionary accounts, which consider the selection for tamer emotional traits (increased approach, decreased withdrawal) of major importance for the emergence of human sociality and cooperation (Hare & Tomasello, 2005).

In light of these proposals, the oxytocin system may represent a candidate system that selective pressures have acted upon during human evolution (Carter, 2014). This viewpoint further raises interesting questions regarding the role that genetic and environmental factors play in programming the oxytocin system and sensitive responding to eye cues during early human development. Indeed, there is recent work to suggest that genetic and environmental factors acting on the oxytocin system impact infants' responses to emotional information from the eyes (Krol, Monakhov, Lai, Ebstein, & Grossmann, 2015). Specifically, 7-month-old infants with a genotype (CC carriers of the *CD38* gene), associated with reduced levels of oxytocin and an increased rate of autism, showed greater looking (attention) to happy eyes and reduced attention to angry eyes. This was the case only when infants with this genotype were exclusively breastfed for longer durations (more than 5 months), but not when exclusively breastfed for shorter durations (less than 5 months). This suggests that early in human development, genetic and environmental factors impacting the oxytocin system differentially modulate attention to social eye cues.

In summary, the work reviewed here has identified oxytocin as a key modulator of sensitive responding to eye cues. This points to neurochemical pathways

that contribute to the detection of eye cues and reading the mind in the eye. The existing work and the continued study of the effects of oxytocin on eye cue responding enable us to build bridges between phylogenetic, ontogenetic, and neural levels of description outlined above and might therefore help in creating a powerful explanatory framework.

Considerations regarding autism

Given what we have seen thus far, the question emerges: What is known about neurodevelopmental profiles associated with atypical responding to eye cues? This leads us to consider the case of autism. Autism spectrum disorder (ASD) is a neurodevelopmental disorder characterized by marked social impairments (Ronald, Happe, & Plomin, 2005). What is notable with respect to the current context is that impaired responding to eyes and eye cues has been described as one of the earliest identifiable warning signs in the development of autism (Elsabbagh & Johnson, 2010; Elsabbagh et al., 2012; Zwaigenbaum et al., 2005). Critically, there is recent work to demonstrate that in autism the orientation to eyes is initially present in young infants but later declines, between 2 and 6 months of age (Jones & Klin, 2013). This suggests that amygdala-based orienting to eyes, at least at an early developmental stage, is in place. It further indicates that the impairment seen in autism may be related to a decline in enhanced attention to eyes and how this decline in attention impacts processes that permit the decoding of emotional, attentional, and mental states associated with brain processes in pSTS and mPFC. There is some evidence from work with infants pointing in this direction. Namely, characteristic differences in the cortical brain responses to eye gaze cues recorded at the age of 6 to 10 months predicted autism diagnosed at 36 months (Elsabbagh et al., 2012). However, a further issue is that according to some accounts, infants that later develop autism, rather than

being impaired in their interpretation of social cues, may in fact be less motivated to engage socially with others (Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2013). This brings up the role that motivational factors play in the development of, and neural responding to, eye cues. Interestingly, work on the effects of oxytocin may speak to this question, because oxytocin has been shown to affect motivational processes as it increases approach behaviors, including the attention to the eye region and eye cues, while reducing withdrawal behaviors (Carter, 2014; Kemp & Guastella, 2011). With respect to autism, children with autism display enhanced brain responses to eye cues after oxytocin administration (Gordon et al., 2013). It is thus possible that atypical patterns in the development of the oxytocin system during infancy account for differences in social motivation and approach behavior, which are also reflected in a reduced sensitivity to eye cues. In fact, as mentioned above, there is recent work to suggest that environmental and genetic factors related to the oxytocin system account for individual differences in the sensitivity to eye cues in infants (Krol et al., 2015). Intriguingly, it is especially those infants that are genetically at a higher risk for autism (CC carriers of the CD38 gene) for whom prolonged durations of breastfeeding are associated with increased attention to prosocial cues (happy eyes) and decreased attention to antisocial cues (angry eyes). Clearly, more work is needed to elucidate the interplay between genes and environment in understanding the development of sensitivity to eye cues and how this relates to risk and resilience regarding certain aspects of the autism phenotype.

Generally, when considering the case of autism it seems important to think more about the purported role of oxytocin in contributing to sensitive responding to eye cues. Specifically, it is possible that feedback loops exist such that oxytocin increases social motivation and engagement through the eyes and social engagement

with others through looking at their eyes increases oxytocin release (Uvnas-Moberg, 1998). Autism may present us with a case where oxytocin levels are lower (Modahl et al., 1998), probably due to genetic factors (Lerer et al., 2010; Lerer et al., 2008) and this results in reduced social motivation and sensitivity to eye cues. Therefore, the feedback loops stimulating the oxytocin system might be disrupted.

Considerations regarding the role of early experiences

Another important issue to consider is what role does early experience with social eye cues play in shaping the responsiveness to eyes cues in humans. With respect to this question, there is an interesting case study of a woman born blind whose cataract was removed when she was 12 years old and who was then tested at 20 years after eye surgery (Ostrovsky, Andalman, & Sinha, 2006). In this case study, the woman showed a remarkable recovery of visual functions as evident in the performance in various visual tests. Interestingly, despite the overall great recovery of visual abilities, there remained a selective impairment in detecting gaze direction from eye cues. Specifically, rather than using eye gaze, the woman relied on head orientation when judging the direction of another person's gaze. This suggests that the ability to respond to eye cues may develop during a sensitive period in development (Lewis & Maurer, 2005). Clearly, this is a tentative suggestion based on a single case study. More work is needed to investigate whether this represents a stable pattern.

A recent study sheds light on the question of what role experience with social eye cues plays in early development by systematically studying sighted infants of blind parents (Senju et al., 2015). This presents an interesting and important case to study, because early social experiences for this group of infants are characterized by a marked limitation to eye cue-based parent-infant interactions. In this study, sighted

infants of blind parents were found to rely significantly less on eye gaze cues while showing otherwise similar performance regarding a number of social and cognitive tests when compared to a control group. Interestingly, this study further showed that this difference becomes more pronounced with development, as seen in a decrease in attention to eye movement and gaze direction between the end of the first year of life and the beginning of the second year of life. This shows how specific experience shapes sensitive responding to eye cues (especially gaze) during infancy. It remains to be seen whether this represents a developmentally stable modification in attention to eye gaze cues or whether it changes and adjusts to the environment when the child spends more time interacting with non-blind adults and peers in addition to their primary caregivers. More generally, this study highlights the importance of considering environmental factors, plasticity and learning when studying the development of eye cue processing.

Considerations regarding additional functions of eye cues

It is important to note that there certainly are other and perhaps related functions that a sensitivity to eyes may serve. For example, sensitivity to eye cues is thought to be of key importance in social learning and especially during natural pedagogical encounters (Csibra & Gergely, 2009), where social gaze information has been shown to facilitate the learning of generalizable information about people and objects (Tummeltshammer, Wu, Sobel, & Kirkham, 2014; Wu, Tummeltshammer, Gliga, & Kirkham, 2014; Yoon, Johnson, & Csibra, 2008). This indicates that eye cues provide a rich source of information relevant for social learning and collaboration.

Moreover, there is a line work showing that sclera color provides important cues involved in perceiving age, health, and beauty in human adults (e.g., Provine, Cabrera, & Nave-Blodgett, 2013; Russell, Sweda, Porcheron, & Mauger, 2014). For example, faces with eyes edited to have redder and yellower sclerae were rated as less healthy, less attractive and older than faces with unchanged sclera color (Provine et al., 2013). Furthermore, in this study, faces with eyes edited to have whiter sclerae were judged to be younger, but not more healthy or beautiful, than the faces with unchanged sclerae. This shows that specific eye cues such as the color of the sclera play a role in the perception of a person.

In summary, there is evidence that, in addition to the functions that have been argued for in the current proposal, human-specific eye cues serve other functions related to social perception and social learning. For future work, it will be critical to investigate the developmental and brain origins of these functions in order to understand to which degree they depend upon mechanisms shared with the mind perception functions put forward in the current proposal or reflect independently instantiated functions.

Integration

This review of the existing work has shown what constitutes uniquely human responding to the eyes, when it develops and how it is implemented in the human brain. We have also seen how this sensitivity to eyes and eye cues might facilitate cooperative behavior in humans, and discussed how this sensitivity to eyes is modulated by the neurohormone oxytocin. This section's goal is to integrate across the phylogenetic, ontogenetic, and neuroscience levels of description in order to arrive at a framework that can comprehensively account for human responding to the eyes.

Comparative work suggests that humans possess a unique sensitivity to eyes and eye cues. This human sensitivity to eyes makes use of the unique morphology of the human eyes and is characterized not only by an increased attention to eyes in general but also by a more effective and broadened utilization of eye cues to detect emotional, attentional, and mental states. Critically, neuroscience work indicates that this sensitivity to eyes is underpinned by a network of brain regions comprising of the amygdala at the subcortical level and pSTS and mPFC at the cortical level, implicated in enhanced attention to eyes and the detection of emotional, attentional, and mental states from eye cues, respectively. Developmental work points to the existence of increased attention to eyes in newborns and indicates that the processes involved in detecting emotional, attentional, and mental states from eyes emerge during the course of the first year of life.

Together this suggests that there are two processes that drive human-specific responding to eyes: one built into the newborn visual orienting system that likely relies on subcortical brain regions such as the amygdala and another one that rapidly develops during infancy supported by cortical brain regions such as the pSTS and mPFC, allowing for the detection of emotional, attentional, and mental states in others on the basis of information present in the eyes or eye region. According to this two-process model, there is one process that ensures privileged attention to information encoded in the eyes and a second that permits for the decoding of this information. Critically, in this model, privileged attention to eyes and scanning of the eye region is assumed to be a prerequisite for the successful detection of emotional and mental states from eye cues. These processes should therefore be viewed as two consecutive and contingent stages of processing information from the eyes. Although this suggests that these two processes occur as two stages one after the other, to date,

there is no direct evidence for this notion. This is probably explained by the fact that methods allowing for the precise (non-invasive) measurement of the timing of brain responses such as ERPs are limited in their spatial resolution and do not detect subcortical sources such as the amygdala. However, there is some evidence from invasive (intracranial) ERP recordings in epilepsy patients to show that amygdala responses precede responses in temporal and prefrontal cortex when processing fearful faces (Krolak-Salmon, Hénaff, Vighetto, Bertrand, & Mauguière, 2004). This suggests that it is possible to examine the exact time course of the brain processes implicated in sensitive responding to social eye cues and thus test the predictions of the proposed two-process model in future studies.

Given that navigating the visual world generally relies upon processes that involve orienting to an object and then recognizing this object (Corbetta & Shulman, 2002; Ungerleider & Haxby, 1994) another critical issue to consider is whether and how the two proposed processes are specific to eyes. The reviewed studies show that the brain regions implicated in the two proposed processes are different from the brain regions generally employed during exogenous visual orienting and visual recognition, supporting the notion that there might be something specific about eyes. However, at the same time, the brain processes involved in processing eyes have been shown to play a more general role in social perception and cognition in humans. Indeed, there is work to show that there is overlapping activity in mPFC when viewing eye contact and hearing somebody call your name (Kampe et al., 2003), suggesting that social cues regardless of modality result in activity in brain regions associated with understanding emotional and mental states. Clearly, more work is needed to directly compare between eye cues and social cues from other modalities to elucidate shared and specific processes related to eye cue processing. Finally, in this

review, we have seen that what is detected during these two processing stages feeds into evaluations and decisions, and thus helps guide and regulate social behaviors. In particular, this review provides empirical evidence for the view that eye cue-based social evaluations facilitate cooperative behaviors.

The research reviewed herein generally supports the notion that much information about other minds can be gleaned from the eyes, and that this information provides a vital basis for initiating, maintaining and regulating social interactions among humans. The argument advanced by this integration is that eyes provide a basis for connecting with other minds. More specifically, processes related to privileged orientation and attention to the eyes may help with detecting the presence of other minds, and processes related to decoding information contained in the eye or eye region helps with reading the contents of other minds. In this context, it is critical to emphasize that although research suggests that a great number of emotional and mental states can be discerned from the eye region (Baron-Cohen et al., 2001), the specific emotional and mental states that can be detected from the eyes and the facial features surrounding the eye are likely limited and the detection of some emotional and mental states has been shown to rely more heavily on other facial or social cues (Aviezer, Trope, & Todorov, 2012; Smith, Cottrell, Gosselin, & Schyns, 2005). Furthermore, it is important to mention that whether information from the eyes is attended to and employed during social interactions also depends on context and prior information (Birmingham, Bischof, & Kingstone, 2008; Buchan, Paré, & Munhall, 2007; Vö, Smith, Mital, & Henderson, 2012; Wiese, Wykowska, Zwickel, & Müller, 2012). It is thus for future research to further specify the conditions under which eyes play a role in social cognition and to identify the limits of what can be ‘read’ from the eyes.

The developmental and neuroscience work presented in this review suggest that this ability to read other minds develops early in infancy. This view is in line with mounting evidence from numerous behavioral studies that, contrary to what was previously thought, attest to infants' mind reading abilities (Baillargeon, Scott, & He, 2010; Reddy, 2008; Woodward, 2009). This is certainly not to say that there is no development in mental state understanding beyond infancy (see Wellman, 2014, for an extensive discussion), but simply to underline that different lines of research converge on the notion that access to other minds is an important and early emerging feature of human social cognition, and that responding to eye cues appears to constitute a prime arena in which this plays out. At this point, it is also important to acknowledge that, despite the mounting evidence for infants' mental state understanding, there still is some debate as to whether infants can reason about others' mental states or might be relying on associative learning mechanisms when succeeding in the various tasks that have probed their mental state understanding (Heyes, 2014). However, the criticism raised mainly applies to behavioral tasks of (false) belief understanding and may thus not hold for the evidence presented in the current analysis. Critically, the current proposal relies on the integration of information from different fields including neuroimaging studies, demonstrating similarity in the brain processes engaged by human infants and adults when processing eye cues. Based on this similarity, it seems unlikely that different mechanisms (representations) are at play in adults than in infants. More generally, the kind of mental state understanding invoked in the current proposal does not require the infant to have an explicit (conceptual) grasp of other minds but might rely on a more direct experience of others' emotional and mental states (Reddy, 2003, 2008). Nonetheless, more work is needed to further specify the exact mechanisms that

underpin sensitive responding to social eye cues in infants and adults. Future work targeted at unraveling the underlying mechanisms might benefit in particular from a more formalized approach including computational modeling (Hamlin, Ullman, Tenenbaum, Goodman, & Baker, 2013; Sevgi, Diaconescu, Tittgemeyer, & Schilbach, in press).

Noticeably, while the emphasis here was on the phylogenetic, ontogenetic, and brain origins of sensitive responding to eyes, eyes are certainly not the only route to understanding other minds. Other sources are equally important for informing us about the presence and content of other minds. For example, there is much work to show that humans use vocal cues in a very similar manner as they use facial and eye cues and sensitivity to voices emerges early in ontogeny (Belin, Fecteau, & Bedard, 2004; Grossmann, 2012). In the congenitally blind the non-availability of visual eye cues may result in a greater emphasis and mastery of responding to vocal cues. Indeed, there is work that supports this idea by showing that congenitally blind adults show enhanced brain responses in the STS to voices and that this activity correlates with performance in a voice discrimination task (Gougoux et al., 2009). Moreover, in certain contexts, vocal cues have been shown to provide more powerful information regarding another person's mind than facial cues (Schroeder & Epley, 2015). Apart from vocal cues, humans may also rely on information provided through touch (Fairhurst, Löken, & Grossmann, 2014; Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006), although when compared to facial and vocal cues, touch as a means for social communication has been relatively neglected. Future work that systematically assesses mind perception and its effects on cooperation by looking at other modalities and by comparing between visual, auditory, and tactile cues is critically needed to specify the role of the eyes in social cognition and behavior.

Nonetheless, the evidence presented in this review suggests that eyes might have a special status with regard to mind perception in humans.

Importantly, eye cues function particularly well during close range interactions without direct physical contact, which are characteristic for many social and collaborative activities in humans (Tomasello et al., 2012). This includes activities such as hunting and gathering (foraging) (Marlowe, 2005), which is considered the primary and ancestral form of subsistence within the genus *Homo* (Lee, 2005). Compared to vocal signaling, coordination through eye cues has the advantage that it can occur silently, making it an ideal form of communication between cooperators during group activities such as gathering and hunting, when at the risk of being noticed by predators or prey. Despite the adaptive advantages with respect to human cooperative activities seen in adults, from a developmental perspective, an early emerging sensitivity to eyes might lay the foundation for being able to identify, choose between, and coordinate with cooperative partners (Tomasello et al., 2005; Tomasello et al., 2012).

All in all, we have seen that when integrating across phylogenetic, ontogenetic, and brain levels of analysis a coherent picture concerning the origins of responding to eyes in humans begins to emerge. The framework presented herein argues for a two-process model that can account for responding to eyes as cues into other minds. According to this model, a first process ensures privileged attention to information encoded in the eyes and is important for the detection of other minds, and a second process permits for the decoding of information contained in the eyes, concerning another person's emotional, attentional, and mental states. This review has shown that this organization is reflected in the developmental emergence and the neural instantiation of these processes. The argument put forward here goes beyond the

description of these processes by suggesting, on the basis of the empirical work surveyed, that the identified processes are likely to serve critical functions in initiating, maintaining and regulating cooperative interactions in humans. Viewing eyes as windows into other minds can therefore be considered a hallmark feature of human social functioning with deep biological roots. It is my hope that the current proposal provides a fertile basis for fostering interdisciplinary research efforts to understand the human mind and will help guide future work into the origins of eye-based social cognition in humans.

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