

Chapter 1

New Frontiers of Investigation in Social Attention

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1.1 Social Attention as a Changing Field of Research

Research into human behavior and its neural bases in general has changed greatly over the past 50 years or so. The earliest studies focused on characterizing behavioral phenomena and teasing apart their behavioral components, in addition to characterizing the timing of neural activity and identifying active brain regions associated with these behavioral observations. More recent studies are beginning to take the pieces of this jigsaw puzzle that were generated from the earlier work to try and put together a picture of embodied cognition that is integrated with activity in multiple brain networks. This latter approach has also changed the way in which laboratory studies are being designed and conducted. The field of social attention has mirrored these changes and in this volume we explore some of the most fascinating new research and also look at unanswered questions—questions that will set the direction for the next decade or so of work in this area.

1.1.1 Initial Studies of Social Attention

Social attention is an intriguing concept—the term is used very frequently in the literature, but rarely does one see it formally defined. The term *social attention* was originally used almost half a century ago (Emery, 2000) to describe the exchange of glances and bodily proximity that distinguish cohesive subgroups of hamadryas baboons, which typically consist of a male and several females, from other individuals

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in the troop (Chance, 1967). The dominant (male) animal is always the focus of attention of subordinate (female) individuals in the group—resulting in a grouping that “underlies or plays a part in all the social relationships by which an animal relates itself to others in a group” (Emery, 2000).

From these original studies of nonhuman primates, the term *social attention* was originally coined to convey the idea of an “attention structure” (appropriate for both human and nonhuman primates) that considers social awareness, as signaled by physical proximity, head and body orientation to conspecifics, as well as dynamic gaze. What was original and novel about the concept of social attention at that time was that attention was being proposed to be a *central part of social organization* (Chance & Larsen, 1976). In those early days of social attention research, many comparative behavioral studies of different nonhuman primates were completed, mainly in the wild, ranging from the savannah environments inhabited by Old World monkeys to the tropical rainforests of the New World. These studies in naturalistic environments indicated that social attention was an important element for any social primate society. In addition, behavioral studies in the laboratory on healthy human infants, children, and adults were also beginning to be performed in group situations or in isolated contexts (Chance & Larsen, 1976).

It is now generally conceded that social attention in humans begins at birth, although there continues to be a lively debate concerning whether this attention occurs due to specialized or more domain-general mechanisms (Nelson, 2001). Regardless, human infants’ social attention to bodies, faces, and eyes develops rapidly during the first year and facilitates their understanding and responses to social behaviors from very early on. By 3–4 months of age, infants develop the ability to follow the direction of gaze or pointing gestures, and this experience eventually contributes to their sharing with others visual attention to various aspects of their environment, a process known as *joint attention* (Corkum & Moore, 1995; Scaife & Bruner, 1975; Tomasello, 1995). In the second year of life, these abilities become more extended and more elaborate, forming a scaffold for the development of language skills and theory of mind (Bakeman & Adamson, 1984; Dunham & Dunham, 1995; Ninio & Bruner, 1978; Tomasello, 1995).

1.1.2 Some Definitions

Throughout this volume a number of terms will be used, which we attempt to define broadly here. The use of the term *social attention* in this volume is taken to refer to where, or what, in the (visual) environment an individual has directed their attention to. We make inferences about where another’s social attentional focus lies from where they point with their fingers, but most often they will “point with their eyes”, (Hadjikhani, Hoge, Snyder, & de Gelder, 2008; Shepherd, 2010) i.e., shift their gaze to their desired focus of visuospatial attention. Head and body position can also be powerful signals as to where social attention is being directed to (Emery, 2000; Langton, Watt, & Bruce, 2000; Perrett, Hietanen, Oram, & Benson, 1992),

and these latter cues are at their most useful when others are at a distance to us, where the direction of gaze in the face might not be seen so clear. Altered social attention is commonly signaled by changes in gaze. An observed *averted gaze* serves to redirect attention *away* from the observed individual and *toward* the new locus of their attention in visual space (Klein, Shepherd, & Platt, 2009).

Another's social attention falling on us, as in a *direct gaze*, can be arousing, particularly if it is sustained. In human subjects, changes in skin conductance response and heart rate variability correlating with increased arousal in response to experiencing direct gaze have been described (Helminen, Kaasinen, & Hietanen, 2011; Ponkanen & Hietanen, 2012). These changes in arousal can be influenced by endogenous factors such as state of anxiety (Wieser, Pauli, Alpers, & Muhlberger, 2009) or by exogenous factors such as one's cultural milieu (Akechi et al., 2013). The abundance of terms in the English language to describe gaze indicates that it is considered to be more than just an incoming visual signal. It is notable that we use verbs that evoke perception in sensory modalities other than vision, or we use verbs to describe actions that accompany the word "gaze." For example, we can "hold" the gaze of others, we "feel" another's gaze upon us, we regularly "follow" or "meet" the gaze of another, and indeed another's gaze can be seen as being "penetrating." If we meet the gaze of another, we engage in a *mutual gaze* exchange (Kleinke, 1986), where we each have become the object of one another's social attention.

Observed gaze aversions in others are thought to trigger a reflexive shift in the observer's visuospatial attention, where the observer's gaze is altered to fall on the same referent in the environment (Friesen & Kingstone, 1998; Itier & Batty, 2009). This induced gaze shift is known as *gaze following* (Butterworth & Cochran, 1980; Corkum & Moore, 1995; Rosati & Hare, 2009). Observed gaze shifts in others can also be regarded as spatial cueing signals, as are arrow cues. Even though both types of stimuli can prime orienting responses in spatial cueing experiments (based on the paradigm developed by Posner (1980)), the social cue represented by the eyes is much more likely to be selected by healthy subjects in the natural environment (Birmingham & Kingstone, 2009).

Gaze following is the cornerstone of joint attention (Itier & Batty, 2009). *Joint attention* is said to occur when two (or more) individuals attend to a common aspect of their (visual) environment during an interaction (Tomasello, 1995). This common focus of attention can be initiated by a change in gaze direction, head orientation, pointing gestures, or verbal cues from one individual that provide the signal to where in the environment the other needs to direct their gaze (or social attention). Joint attention "is not just a geometric phenomenon concerning two lines of visual orientation," but requires that both participants *know and monitor* each other's visuospatial attention to the common aspect of the environment (Tomasello, 1995). For example, typically the individual who initiates the signal for another to gaze to a feature, or person, in the environment will usually follow-up the initial signal with a gaze back to the other person to confirm that their (social) attention has actually been redirected to the desired focus in the environment.

Just because an individual chooses to change their gaze to focus on a particular location in their environment, this may not necessarily be an overt signal to initiate

social or joint attention with another. If two observers happen to be looking at the same common point in the environment in the absence of a social interaction or context (see Lachat, Hugueville, Lemarechal, Conty, & George, 2012), this is not considered to be joint attention. Similarly, a daydreamer who is engaged more by their inner mental life than their external surroundings will also show changes in eye position that are driven by their introspections and not by fixations to features in the surrounding visual environment (Schooler et al., 2011). More importantly, someone wanting to deceive another might actually gaze away from their actual point of interest (e.g., Klein et al. (2009)). Hence, one's direction of gaze is not necessarily always an accurate signal of another's apparent social attention. In this sense, social attention always has to be evaluated in terms of some (environmental) context.

As discussed above, when one gazes directly at an individual during a social interaction, then it is said that their *social attention* is directed at the individual being gazed at, because the individual being gazed is a likely *target for a current or future behavior*, in addition to being the likely current focus of their directed visual attention. Direct gaze is a very salient social stimulus, as it can signal a number of different socially relevant cues. It is of particular interest, if it occurs after an explicit visual cue in the form of a gaze aversion that serves as a pointing gesture. In contrast, an averted gaze may signal social rejection, or wanting to avoid social contact or engagement. In addition, a sudden gaze change, away from the observer, could be a potential signal of danger or threat (Hadjikhani et al., 2008; Haxby, Hoffman, & Gobbini, 2002).

Gaze signals are important visual cues not only in humans but also in animal and primate societies (Emery, 2000; Klein et al., 2009; Kleinke, 1986), as they can facilitate social learning (Garipey et al., 2014) as well as being powerful modifiers of behavior (Bethell, Holmes, Maclarion, & Semple, 2012; Brumm, Kipper, Riechelmann, & Todt, 2005). For example, chimpanzees have been observed to engage in certain risky behaviors only when they are aware that the gaze of dominant conspecific is occluded (Tomasello, Call, & Hare, 2003). Apes and macaques have even been described to hide their facial expressions behind their hands when they are in the line of sight of other conspecifics (Tanner & Byrne, 1993; Thunstrom, Kuchenbuch, & Young, 2014; de Waal, 1986). Overall, as already noted earlier, while direction of gaze can signal a change in another's social attention, both the social and nonsocial contexts in which the gaze change occurs must be taken into account to successfully interpret the intentions underlying the observed change in gaze.

Most nonhuman primate eyes have relatively small luminance and contrast differences between the iris and sclera; however, in human primates, this visual feature has been amplified by a distinct white sclera and colored iris (Rosati & Hare, 2009). Hence, a change in this high-contrast visual cue (e.g., a gaze aversion) can be well seen even at a distance from the observer (Emery, 2000). Given the importance of the gaze signal for the human primate, much of this volume will deal with social/joint attention as signaled by gaze changes in developing and mature human subjects who have normal or aberrant social cognition. However, we also need to consider the role of objects and goal-directed behaviors in episodes of joint attention—with this synthesis being examined in a few of the chapters of this volume. We also

acknowledge that social attention includes much more than the themes examined in our volume. For example, research in nonhuman primates clearly shows that social attentional phenomena (in terms of behavior and neural correlates) show parallels to human subjects, and are crucial for understanding social hierarchy (Chance & Larsen, 1976; Emery, 2000; Garipey et al., 2014; Klein et al., 2009; Kleinke, 1986).

How has the field of social attention changed since it first developed almost 50 years ago? Initial laboratory-based investigations in human subjects focused on behavior recorded by movie camera, and then later added eye tracking. However, initial studies of eye tracking were performed not to evaluate social attention, but to investigate other viewing phenomena. As early as the 1950s, Yarbus (1967) had been experimenting with reflected light beams to record sequences of fixations when observers were viewing pictures, and this work along with that of Buswell from 1935 established a foundation for studying how the eyes move to, and settle on, different features in a visual scene (Buswell, 1935; Land & Tatler, 2009). The very elaborate laboratory setup established by Yarbus for recording eye movements was, however, difficult to implement in nonexpert hands. In the 1970s, eye-tracking research began to expand rapidly as developments in technology made it possible to simplify the laboratory recording setup, and this was especially true for research on reading (Rayner, 1998).

Although some theorists were inclined to claim that eye tracking and overt attention were a “window into the mind,” (e.g., Just & Carpenter, 1980), this view was difficult to reconcile with new findings on covert attention revealing that attention is not always directed toward where the eyes are looking (Posner, 1980). Beginning in the 1990s, eye tracking began to be used in research related to faces and social cognition (Vecera & Johnson, 1995). More recent research and the development of new techniques, such as gaze-contingent eye tracking (Duchowski, 2002), have enabled researchers to resolve a number of methodological challenges and begin to address new questions relating to cognitive and social processes. Today eye tracking is becoming as common as other behavioral measures when studying processes such as social attention and social cognition in infants and adults (e.g., Gredeback, Johnson, & von Hofsten, 2010; Torralba, Oliva, Castelhana, & Henderson, 2006; Vo, Smith, Mital, & Henderson, 2012). Importantly, eye tracking can yield insights not only into where the subject is looking, but also their pupil size can signal their state of autonomic arousal (Steinhauer, Siegle, Condray, & Pless, 2004; Yoss, Moyer, & Hollenhorst, 1970).

Noninvasive electroencephalography (EEG), or the ability to record the spontaneously occurring electrical activity of the brain from the scalp, has been around for many years, with the discovery of the major electrical rhythms of the brain occurring in the earlier part of the twentieth century (Berger & Gloor, 1969; Jasper & Andrews, 1938; Walter, 1936). EEG was initially used mainly for clinical purposes, but as stimulus-elicited changes in the EEG (i.e., event-related potentials or ERPs) were identified with methods such as averaging (Dawson, 1947) EEG began to be used in psychophysiological research. Magnetoencephalography (MEG), a technique that records the changing magnetic fields emitted by the brain, was pioneered in the early 1970s (Cohen, 1972). Functional neuroimaging methods such as positron emission

tomography and functional magnetic resonance imaging (fMRI) allowed focal activation in the brain to be visualized for the first time as human subjects performed various activation tasks in the late twentieth century (e.g., Belliveau et al., 1991; Petersen, Fox, Posner, Mintun, & Raichle, 1989). In line with these groundbreaking developments in technology, a brain-behavior line of investigation developed and spawned new disciplines such as cognitive neuroscience (Churchland & Sejnowski, 1988) and social neuroscience (Cacioppo, 1994; Cacioppo, Berntson, Sheridan, & McClintock, 2000). Not surprisingly, EEG/MEG approaches to assessing the brain bases of social attention were implemented more frequently (Mundy, Card, & Fox, 2000; Puce, Smith, & Allison, 2000), as were studies (George, Driver, & Dolan, 2001; Puce, Allison, Bentin, Gore, & McCarthy, 1998). EEG/MEG methods are particularly attractive in that they can provide neural measures of perception/cognition (and social attention) in preverbal humans (Hoehl & Striano, 2010; Hoehl, Reid, Parise, Handl, Palumbo, & Striano, 2009; Mundy et al., 2000).

Overall, there have been many dramatic changes to the practice of science over the last 50 years, which have greatly impacted research into social attention. Next we examine a number of major scientific themes that are relevant to the field of social attention today, and which are covered in the chapters of this volume.

1.1.3 *Emerging Themes*

Social attention is important in its own right, because it is one of the key pillars in the study of social cognition and theory of mind. In the late twentieth century, the study of social attention became an established area in cognitive and social neuroscience and continued to be an important focal point for research identifying the component brain *regions* that are necessary when evaluating another's social attention (i.e., from a localizationalist perspective). Areas of brain, such as the superior temporal sulcus, amygdala, and orbitofrontal cortex, were repeatedly shown to be particularly sensitive to social attention, as signaled by eye gaze, in both human and nonhuman primates (Baron-Cohen, 1995; Brothers, 1997). Knowing what brain regions are active in social attention, however, could not answer questions regarding the neural mechanisms underlying social attention. To this end in the twenty-first century, neuroimaging research has shifted its focus toward examining the behavior of active brain *networks* that underlie the deployment of social attention, as well as other social, affective, and cognitive processes (Sporns, Chialvo, Kaiser, & Hilgetag, 2004; Sporns, Tononi, & Kotter, 2005). This network-type approach is currently a strong driving force in cognitive and social neuroscience, where the functional and effective connectivity between component brain regions making up a network is beginning to be routinely investigated. Importantly, dynamic temporal functional connectivity across networks is also becoming an important area of study. Preliminary evidence indicates that different networks make transient connections with one another during the course of performing a task, or even during quiet rest (Breakspear, 2004; Zalesky, Fornito, Cocchi, Gollo, & Breakspear, 2014). These studies of dynamic functional connectivity will continue to be important in the future as

they will be able to help provide an understanding of how various structures in active brain circuits interact with one another during the course of executing different tasks and goals (Medaglia, Lynall, & Bassett, 2015). Social attention research will greatly benefit from these new network-based research approaches.

The quest to study the neural correlates/networks of social attention extends from the healthy brain to the brains of individuals who have neuropsychiatric disorders, such as ASD and schizophrenia (Bush & Kennedy, Chap. 7, this volume). Similarly, behavior (including eye tracking) and brain activity (as assessed by neurophysiological and hemodynamic methods) have shown some interesting differences between neurotypical individuals and those affected by ASD and schizophrenia. Some of these studies suggest that neurotypical and non-neurotypical individuals might achieve similar behavioral goals by using quite different brain pathways. Developmental studies have also begun to focus on the neural correlates of these processes. The developing human brain appears to harbor a sensitivity to faces, eyes, hands, as well as to situations where the meaning of a simple social interaction needs to be interpreted (Bertenthal & Boyer, Chap. 2; Reid & Dunn Chap. 3, this volume). A consistent theme throughout the entire 50-year period in the study of social attention has been the attempt to generate a complete behavioral account for the deployment of social attention in an individual, as well as the evaluation of social attention in another. Experimental paradigms are gradually becoming more complex as investigators increasingly attempt to create ecologically valid paradigms so as to mimic the social interactions that might occur in real-life situations (Nasiopoulos, Risko, & Kingstone Chap. 5; Bush & Kennedy Chap. 7, this volume).

Brain Pathways for Social Attention

Alternate brain pathways for the flow of social information, particularly with respect to social attention, exist in the primate brain (Klein et al., 2009). On the one hand, visual information traveling via a subcortical route (e.g., to extrastriate cortex via the pulvinar nucleus and superior colliculus, and amygdala) is processed rapidly and travels to extrastriate cortex, and is typically not amenable to conscious awareness (Garvert, Friston, Dolan, & Garrido, 2014; Morris, Ohman, & Dolan, 1999). On the other hand, social information traveling via a cortical route (via the lateral geniculate nucleus) to striate cortex is available for conscious evaluation and can be processed and manipulated. This information is passed on to other regions engaged in more integrative processes that allow the interpretation of the mental states, such as the goals and intentions of conspecifics. Not surprisingly, the neural network for processing faces and eyes is extensive and includes at least six highly specialized regions responsible for perception of identity, head and gaze direction, and facial expressions (Allison, Puce, & McCarthy, 2000; Haxby & Ida Gobbini, 2008; Haxby, Hoffman, & Gobbini, 2000; Ishai, 2008). All of this visual information is rapidly and automatically processed and contributes to higher-level interpretations of others' social behaviors. The similarity between the structure and function of the human and nonhuman primate social brain provides a model system for more

invasively studying the analogs of the neural correlates of human social attention and social cognition (e.g., Materna, Dicke, & Thier, 2008)).

The human “social brain” is proposed to consist of four brain networks (Stanley & Adolphs, 2013) (see also Puce et al., Chap. 4, Fig. 1, this volume) that are selectively engaged to different degrees in various aspects of social interactions. Social attention actively engages two of these networks: the so-called mentalizing network and amygdala network. Within these two networks crucial brain regions such as the superior temporal sulcus, the fusiform gyrus, and amygdala play a key role in evaluating an incoming social stimulus. Social attention stimuli are processed quite rapidly in the brain—typically the main differentiation in neural activity occurs around 170–220 ms post-gaze change (Puce et al., 2000), and activity can persist up to almost a second after a gaze change has been viewed, allowing other subsequent behaviors associated with the gaze change to be put into a social context (Ulloa, Puce, Hugueville, & George, 2014). Interestingly, the brain processes dynamic eye movements differently than dynamic mouth movements, even though neural activity to each movement type shows identical temporal characteristics. The latter appear to engage neural mechanisms that are active in evaluating biological motion, whereas the former engage mechanisms that are sensitive to local low-level changes in visual space (Rossi, Parada, Kolchinsky, & Puce, 2014; Rossi, Parada, Latinus, & Puce, 2015). The way this activity ultimately plays out in relation to gaze changes might also depend on the type of information processing mode that the brain is in—a *default* (nonsocial) mode or a *socially aware* mode (see Puce et al., Chap. 4, this volume). In the former, information is processed automatically and this mode is typically used in implicit processing of social attention stimuli. This mode is likely to be active most of the time in daily life, and in some circumstances the information that is gathered in this mode might not be available to conscious awareness. In the latter, top-down processes relevant to the experienced social situation ensure that the information is processed consciously and appropriately with respect to relevant behavioral goals. Not surprisingly, this mode would be active during social interactions. It is tempting to speculate that these two putative modes of processing social information related to the eyes (default and socially aware modes) might correspond to information flow in respective subcortical and cortical pathways.

Automaticity of the Processing of Social Attention Stimuli

In a number of chapters in this volume, the idea is put forward that eyes/social attention stimuli are processed automatically and that information might not be available to conscious awareness (Bertenthal & Boyer, Chap. 2; Puce et al., Chap. 4; Bush & Kennedy, Chap. 7, this volume). The need to focus on the face and, in particular, the eyes, appears to be a natural bias we have when we examine a complex scene that has both people and objects in it (Nasiopoulos, Risko, & Kingstone, Chap. 5, this volume). On the basis of the neuroimaging literature, it is likely that activity in the amygdala may play a prominent role in the generation of these automatic processes. These automatic processing mechanisms may be lacking in individuals with ASD/

autism as they typically spend less time looking at the eyes in a face, or are less likely to look toward the eye region. This can be seen in adults as well as in adolescents and children—signaled most clearly by differences in the “first fixation” in a social scene in ASD/autism relative to typically developing individuals (Schulz, Jones & Klin Chap. 6; Bush & Kennedy Chap. 7, this volume).

Typical Development of Human Social Attention and Joint Attention

Bertenthal and Boyer in Chap. 2 of this volume examine the development of social attention and joint attention during the first year after birth. The idea that selective attention is a dual process is stressed: Initially, shifts of attention are reflexive and driven by the external cues provided by the environment. Later, as the brain develops, the ability to choose where to direct one’s selective attention (and social attention) comes on line, allowing the child to engage in joint attention. According to most theorists (e.g., Carpenter & Call, 2013; Tomasello, 2008), joint attention represents a shared understanding of the intentions of self and other and is crucial for the future learning of actions, the development of language, and the ability to predict the goals and intentions of others. Just as critical, however, is the role of the child’s social cognitive development in educating attention, which is why it is necessary to consider the reciprocal development of social attention and social understanding.

Bertenthal and Boyer (Chap. 2, this volume) first examine the ability of healthy infants to respond to social cues signaled by stimuli such as gaze, head orientation, vocalizations, and pointing (with the fingers). Joint attention, as initiated by finger pointing as well as changes in gaze, is a particular focus in this chapter. Recent research indicates that the ability of an infant to follow the direction of a pointed finger precedes the ability to generate a finger point by quite a number of months. The ability of the infant to perceive important social cues leads to the subsequent ability to select and direct their attention toward the actions of others. As discussed by Bertenthal and Boyer (Chap. 2, this volume) as well as Schulz, Jones, and Klin (Chap. 6, this volume), human infants not only perceive, but also prefer stimuli with social adaptive value. This initial preference ensures that infants will devote considerable attention to faces and eyes and through this experience will gradually learn about the social behaviors and putative mental states of others. The task of learning about the social world is often simplified by testing infants’ attention to faces and eyes in isolation, but this approach runs the risk of misrepresenting infants’ responses in more cluttered and naturalistic environments that are filled with multiple people and objects. Thus, it is important to also study how infants’ attention to actions and their goals are processed in more visually cluttered environments that resemble daily life. It is somewhat surprising that only recently have image statistics been gathered of what typical infants in their first year of life observe in daily life. Interestingly, initially their visual input prominently features the faces of several individuals that are most involved in their care (Jayaraman, Fausey, & Smith, 2015), and later in their first year the visual input features their own and others’ hands as they begin to interact with objects in their environment and learn about their actions (Jayaraman, Fausey, & Smith, 2013).

The attention to actions introduces another theme of considerable significance in studying how infants learn about others' actions and intentions. Infants learn a great deal about themselves and others from observing the effects of their own actions as well as those of others (Bertenthal & Campos, 1990). The discovery of mirror neurons in the monkey's brain by Rizzolatti, Fadiga, Gallese, and Fogassi (1996) and potentially homologous findings in humans (Decety et al., 1997) stimulated a great deal of new research and debate regarding action understanding and its social significance (see also Hickok, 2009). In recent years, there has been growing interest in studying the relation between action understanding and motor experience, and the results suggest that action understanding is greatly facilitated by the availability of motor representations of the corresponding actions (Woodward & Gerson, 2014). Curiously, this aspect of the literature has rarely made contact with research on the development of social attention even though theories, such as the premotor theory of attention (Rizzolatti, Riggio, & Sheliga, 1994), suggest compelling reasons why action understanding will depend intimately on the observer's attention to the actors' social as well as instrumental behaviors. This missing link in the literature is addressed by Bertenthal and Boyer (Chap. 2, this book), who discuss research on how infants' action understanding is modulated by visual attention.

Joint attention has also been studied in the typically developing brain with EEG/ERP methods (Reid & Dunn, Chap. 3, this volume). Specialized brain activity emerges early in development to faces, eyes, and shared referents during joint attention, i.e., in the form of slow ERP responses that decrease in latency and amplitude with increasing age and development. This research converges with behavioral research to demonstrate that infants are biologically prepared to attend to faces and eyes early on in life. Differences in ERP components, such as N170 and Nc, and the positive slow wave (PSW) as a function of stimulus condition indicate that by 4 months of age infants are processing direct and averted gaze differently. Moreover, these neural processes are modulated by facial expression, suggesting that infants are already sensitive to contextual differences by this age. One of the key advantages of neurophysiological research is that the EEG signal can be broken down into different components in the temporal domain with millisecond accuracy, which thus provides greater precision in elucidating what develops over time. For example, infants' differential responding to direct versus averted gaze is indexed by the latency and amplitude of a negative component corresponding to the N170 ERP in adults, but the modulation of eye gaze via facial expression is indexed by the PSW, suggesting that quite different neural mechanisms contribute to this latter process.

One of the key contributions of the chapter by Reid and Dunn (Chap. 3, this volume) is to show that neural processing of objects is modulated by joint attention. For example, Parise, Reid, Stets, and Striano (2008) tested 5-month-old infants' responses to an object that had been previously introduced with, or without, joint attention between the experimenter and the infant. While infants viewed the object, EEG was recorded, and the mid-latency negative component (Nc) showed a greater negative response if this testing followed the joint attention condition (Parise et al., 2008). Converging evidence from other studies supports these results, which, when taken together, suggest that infants are processing some of the social-communicative

information associated with joint attention at a much younger age than is typically reported for joint attention. This result, revealing earlier processing of objects than suggested by behavioral studies, is a common finding with electrophysiological measurements of brain activity, but the challenge is to map these findings onto behavioral and cognitive developments. At least with regard to joint attention to objects, these findings suggest that social attention facilitates the processing of objects and contributes to infants learning about their structural and functional properties. As such, these findings converge with the views of Bertenthal and Boyer (Chap. 2, this volume) that the visual exploration that occurs during joint attention contributes to infants' learning about the social and physical world.

Aberrant Human Social Attention: in Developing and Mature Humans

In a number of neuropsychiatric disorders, such as autism, ASD, and schizophrenia, individuals may experience difficulty in attending to informative social cues or reading the information provided by these cues. Aberrant social attention in the developing brain is discussed by Schulz et al. in Chap. 6 of this volume, whereas that in the more mature brain is dealt with by Bush and Kennedy in Chap. 7 of this volume.

Schulz et al. (Chap. 6, this volume) propose that an early attentional focus on the human face and eyes occurs with the information being processed by subcortical pathways during the first month or two of life. With subsequent development there is a switch from subcortical to cortical pathways, which is accompanied by a transient behavioral decrease in attentional focus on eyes/face in the typically developing individual. In individuals who subsequently develop autism/ASD the switch may well occur at this same time, but it is likely that the cortical pathways are not functioning correctly. Schulz et al. argue that the development of brain pathways is shaped, or "canalized", by incoming sensory experiences. Given that in typical development the focus is on people's faces and eyes, the bias created for this type of visual input sets into play the development of further specialization in the brain as a function of the interactions between the infant's visual experiences and brain maturation. Conversely, in autism/ASD the preference for faces is initially as strong as it is in typically developing infants, but it declines during the first year, whereas this preference increases for typically developing infants. It is hypothesized that these early abnormalities in social attention disrupt infants' formative social experiences with caregivers and others and result in cascading downstream effects that affect typical neural, cognitive, and behavioral development.

In the chapter by Schulz et al., research is also reviewed, which leads to a novel hypothesis as to why children with ASD show greater interest in the synchrony between speech and mouth movements than typically developing children. Rather than suggesting that these infants prefer looking at the mouth relative to the eyes, this research reveals that these children are likely to be biased to attend to audiovisual synchrony *in general*. Audiovisual synchrony is present in movements of the face and associated vocalizations, and thus may explain the focus on the mouth that

many individuals with ASD are said to have. The different (nonsocial) focus in ASD therefore sets into motion the development of brain pathways that are appropriate to processing the incoming sensory input, but which are likely to differ relative to those individuals with a neurotypical profile. If this is the case, then the same visual input is likely to be processed by potentially different mechanisms, modes, or even brain pathways in a neurotypical individual relative to one who has ASD. Data from multiple studies indicate that behavior is very different in neurotypical versus ASD adults, adolescents, and children (Bush & Kennedy, Chap. 7, this volume).

Bush and Kennedy (Chap. 7, this volume) make clear that disruptions in social attention among children with ASD persist into adulthood, and these social deficits continue to impact their behavior, cognition, and brain functioning. The deficits associated with ASD fall along a spectrum of social behaviors and there is considerable heterogeneity in this subject population, which makes the assessment of common root causes extremely challenging. Three categories of explanations are considered for these observed differences:

- (1) behavioral, cognitive, and neural factors;
- (2) altered developmental trajectories;
- (3) real-time processing of social behavior modulated by (social) attention.

Currently, it is difficult to reach any consensus on a potentially plausible and correct explanation because of the many inconsistencies and contradictions in the literature. However, Bush and Kennedy focus on aberrant social attention and convincingly demonstrate that these deficits have downstream consequences resulting in neural and behavioral abnormalities that manifest with more complex social processes. One of the important contributions of this chapter is to illustrate why revealing differences between neurotypical and ASD adults often requires extremely sensitive measures across multiple assessment methods, such as those provided by eye tracking and neuroimaging while individuals engage in complex tasks.

In spite of some residual reservations about the utility of eye tracking for studying attention, this measure is ideally suited for investigating social attention because it records not only what observers look at, but also when. As Bush and Kennedy point out, global measures of visual attention may not reveal any differences between neurotypical and ASD adults, because the differences are confined to specific moments or specific features that are only looked at very briefly. The most informative social cues are sometimes the most fleeting and subtle, and therefore it requires very detailed measures of attention that have high temporal resolution to gather this information. A related point is that these subtle cues or more complex situations are typically not reproduced in laboratory experiments, and thus they tend to greatly underestimate the differences between neurotypical and ASD adults.

The deficits in social attention observed in individuals with ASD could be either a function of aberrant processing of the input, or the deficits might be associated with higher-level functions, such as theory of mind—an important function of the social brain. To adjudicate between these interpretations, it is necessary to consider both the behavioral and neural correlates of these processes. As already noted, the mentalizing and amygdala networks in the brain are key components for the

successful deployment of social attention. Within these two networks, three core brain regions are considered:

- (1) the fusiform face area (FFA);
- (2) the amygdala;
- (3) the superior temporal sulcus (STS).

Results from existing neuroimaging studies suggest that it is insufficient to simply measure the level of activation in these regions, because this is often a consequence of the level of attention devoted to the social stimulus (e.g., face or eyes). In addition, the *interactions* between these three core brain regions need also to be considered. Clearly, these findings have important implications for therapies related to the treatment of ASD.

Social Attention vs. Social Cognition

One of the most important implications emerging from Chap. 7 by Bush and Kennedy is that it is clearly necessary to distinguish between social attention and social cognition when studying ASD. As we have indicated earlier, social attention is the crucial front-end to all higher-level social processes, including the recognition of emotions and others' mental states (theory of mind). It is obvious that it is necessary for observers to access social information before they can interpret it. Converging evidence suggests that deficits in social attention are at least sometimes the culprit for misunderstanding others' social behaviors, and thus we cannot assume what is the cause and what is the consequence of ASD without independently assessing both social attention and social cognition. Similar conclusions about a reciprocal relation between social attention and social cognition are discussed by Bertenthal and Boyer (Chap. 2, this volume).

Social learning represents an important link between social attention and social cognition. It is repeatedly emphasized in this volume that our social knowledge depends on our social experiences, but the meditational process by which this occurs is often assumed but not directly studied. It should also be noted that processes involving social learning are also extremely important for the normal development of spoken language (Tomasello, 2008).

Social Presence

Nasiopoulos, Risko, & Kingstone in Chap. 5 present the idea of social presence and examine how it affects social attention. *Social presence* is defined as the influence of the physical presence of another on an individual's behavior, when all other influences have been removed. Interestingly, the effects of social presence are task dependent. For simple tasks, such as skilled motor actions, there is a *positive effect* of social presence on behavior. In contrast, for complex tasks that typically require flexible and varied behaviors, *negative effects* of social presence on behavior have

been consistently reported. In particular, overt task-related behaviors in individuals can be strongly modulated by social presence if the task in question has a personally significant element for the subject who is performing the task. Personal significance can be driven by avoidance of embarrassment (perhaps because of a lack of skill) or by generating a favorable impression of oneself to others.

A related, but more subtle, effect to social presence is *implied presence*. Here, environments that have a closed-circuit television recording setup, or a one-way window, where the subject knows that others are watching them, can also generate these differences in task-related behaviors. Most typically, the individuals who feel that they are being watched will be more likely to adhere to social norms, or will engage in behaviors that potentially will increase their social desirability. Interestingly, the effects of implied presence can also occur with displays of isolated, disembodied pairs of eyes. The implications of this last point are far reaching and there is at least one case study of advertisers manipulating the direction of eyes appearing on a product to increase sales (Musicus, Tal, & Wansink, 2015).

Does social presence affect gaze? It should be remembered that gaze serves a dual function: the eyes are used both to collect information and to communicate with others. Nasiopoulos, Risko, and Kingstone (Chap. 5, this volume) also examine how looking behavior can be influenced by social presence, by using experimental manipulations where the subject wears an eye tracker while they interact with their environment. They demonstrate some interesting effects on looking behaviors whereby subjects will vary the amount of monitoring they do on their own looking behavior, following a reduction of implied social presence via a habituation-type manipulation. The described studies underscore the importance of integrating social psychological variables in the study of social attention, as unexpected changes in behavior might be observed when running paradigms in the laboratory because of the presence of experimenters.

Using Naturalistic Task/Environments to Evaluate Social Attention (and Social Cognition)

Laboratory-based visual stimuli in social attention experiments have typically consisted of (static) images of isolated faces, and are unnatural/unrealistic and do not have the richness of real-world visual environments (Bertenthal & Boyer, Chap. 2; Puce et al., Chap. 4; Nasiopoulos et al., Chap. 5; Bush & Kennedy Chap. 7, this volume). When behavior is compared between impoverished laboratory-based stimuli and real-world environments, quite different types of results related to social attention are evidenced by eye-tracking data (Nasiopoulos et al., Chap. 5, this volume). Specifically, when neurotypical research subjects look at stimuli in the laboratory that are presented on a computer screen, such as static images of directly gazing faces, they typically focus on, and scrutinize, the face and the eyes. In contrast, when subjects are walking around in a real-life environment they will typically only scrutinize the faces and the eyes of others when that individual is suitably far away from them—subjects will tend to avoid gazing at the faces and eyes of strangers if

they encounter an approaching individual. Therefore, looking behavior in a laboratory experiment risks being very different (and indeed could be completely opposite) to that which occurs in a real-life situation. In particular, it appears that gaze following and also gaze cueing behavior in real life appears also to be very different to that observed in the laboratory with isolated, static computerized stimuli. This is a very concerning issue for the existing literature dealing with social cognition in healthy subjects. Notably, laboratory-based studies of individuals with social attention deficits, such as those with ASD, often do not show deficits, completely in contrast to what those individuals experience in real life. Not only is there a difficulty in orienting to a rapid, fleeting social stimulus in a busy visual environment, but also the focus of interest in a complex scene may well be quite different to that of a neurotypical individual. The studies of Nasiopoulos et al. (Chap. 5, this volume) raise these somewhat controversial, but nevertheless critical, questions.

These above questions not only apply to studies of the mature brain, but also are crucial in studies of development (Bertenthal & Boyer Chap. 2; Schulz et al., Chap. 6; Bush & Kennedy Chap. 7, this volume). In this vein, important refinements in experimental procedures in infant studies, such as gaze-contingent cueing, allow significantly greater numbers of trials to be collected in behavioral and eye-tracking studies (Bertenthal & Boyer, Chap. 2, this volume), and thus provide new opportunities for conducting developmental investigations.

Future Challenges and Issues over the Next Decade in Social Attention Research

As already noted, the development of new technologies and new scientific fields has vastly impacted research into social attention. The change in reductionist philosophy in brain-mapping studies (in the later twentieth century) to a more holistic network-driven approach in the twenty-first century is also likely to change the way experimenters design new experiments and formulate scientific conclusions. Bertenthal and Puce (Chap. 8, this volume) attempt to speculate as to how the field might change in the next decade or so, taking into account the latest developments not only in social attention research, but also in science and technology more generally.

References

- Akechi, H., Senju, A., Uibo, H., Kikuchi, Y., Hasegawa, T., & Hietanen, J. K. (2013). Attention to eye contact in the west and east: Autonomic responses and evaluative ratings. *PLoS One*, *8*, e59312.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, *4*, 267–278.
- Bakeman, R., & Adamson, L. B. (1984). Coordinating attention to people and objects in mother-infant and peer-infant interaction. *Child Development*, *55*, 1278–1289.
- Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind*. Cambridge: MIT Press.

- Belliveau, J. W., Kennedy, D. N. Jr., McKinstry, R. C., Buchbinder, B. R., Weisskoff, R. M., Cohen, M. S., Vevea, J. M., Brady, T. J., & Rosen, B. R. (1991). Functional mapping of the human visual cortex by magnetic resonance imaging. *Science*, *254*, 716–719.
- Berger, H., & Gloor, P. (1969). *On the electroencephalogram of man: The fourteen original reports on the human electroencephalogram, translated from the original German and edited by Pierre Gloor*. Amsterdam: Elsevier.
- Bertenthal, B., & Campos, J. J. (1990). A systems approach to the organizing effects of self-produced locomotion during infancy. *Advances in Infancy Research*, *6*, 51–98.
- Bethell, E. J., Holmes, A., Maclarnon, A., & Semple, S. (2012). Evidence that emotion mediates social attention in rhesus macaques. *PLoS One*, *7*, e44387.
- Birmingham, E., & Kingstone, A. (2009). Human social attention: A new look at past, present, and future investigations. *Annals of the New York Academy of Sciences*, *1156*, 118–140.
- Breakspear, M. (2004). “Dynamic” connectivity in neural systems: Theoretical and empirical considerations. *Neuroinformatics*, *2*, 205–226.
- Brothers, L. (1997). *Friday’s footprint: How society shapes the human mind*. Oxford: Oxford University Press.
- Brumm, H., Kipper, S., Riechelmann, C., & Todt, D. (2005). Do Barbary macaques ‘comment’ on what they see? A first report on vocalizations accompanying interactions of third parties. *Journal of Primatology*, *46*, 141–144.
- Buswell, G. T. (1935). *How people look at pictures. A study of the psychology of perception in art*. Chicago: The University of Chicago Press.
- Butterworth, G., & Cochran, E. (1980). Towards a mechanism of joint visual attention in human infancy. *International Journal of Behavioral Development*, *3*, 253–272.
- Cacioppo, J. T. (1994). Social neuroscience: Autonomic, neuroendocrine, and immune responses to stress. *Psychophysiology*, *31*, 113–128.
- Cacioppo, J. T., Bertson, G. G., Sheridan, J. F., & McClintock, M. K. (2000). Multilevel integrative analyses of human behavior: Social neuroscience and the complementing nature of social and biological approaches. *Psychological Bulletin*, *126*, 829–843.
- Carpenter, M., & Call, J. (2013). How joint is the joint attention of apes and human infants? In: H. S. Terrace & J. Metcalfe (Eds.), *Agency and joint attention*. New York: Oxford University Press.
- Chance, M. R. A. (1967) Attention structure as the basis of primate rank orders. *Man [Royal Anthropological Institute of Great Britain and Ireland]*, *2*, 503–518.
- Chance, M. R. A., & Larsen, R. R. (1976). *The social structure of attention*. London: Wiley.
- Churchland, P. S., & Sejnowski, T. J. (1988). Perspectives on cognitive neuroscience. *Science*, *242*, 741–745.
- Cohen, D. (1972). Magnetoencephalography: Detection of the brain’s electrical activity with a superconducting magnetometer. *Science*, *175*, 664–666.
- Corkum, V., & Moore, C. (1995). Development of joint visual attention in infants. In: C. D. Moore & J. Philip (Eds.), *Joint attention: Its origins and role in development* (pp. 61–84). New York: Lawrence Erlbaum Associates.
- Dawson, G. D. (1947). Cerebral responses to electrical stimulation of peripheral nerve in Man. *Journal of Neurology Neurosurgery and Psychiatry*, *10*, 134–140.
- Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., Fazio, F. (1997). Brain activity during observation of actions. Influence of action content and subject’s strategy. *Brain: A Journal of Neurology*, *120*(Pt 10), 1763–1777.
- Duchowski, A. T. (2002). A breadth-first survey of eye-tracking applications. *Behavior Research Methods, Instruments, & Computers*, *34*, 455–470.
- Dunham, P. J., & Dunham, F. (1995). Optimal social structures and adaptive infant development. In: C. D. Moore & J. Philip (Eds.), *Joint attention: Its origins and role in development* (pp. 159–188). New York: Lawrence Erlbaum Associates.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, *24*, 581–604.

- Friesen, C. K., & Kingstone, A. (1998). The eyes have it!: Reflexive orienting is triggered by non-predictive gaze. *Psychonomic Bulletin & Review*, *5*, 490–495.
- Gariepy, J. F., Watson, K. K., Du, E., Xie, D. L., Erb, J., Amasino, D., & Platt, M. L. (2014). Social learning in humans and other animals. *Frontiers in Neuroscience*, *8*, 58.
- Garvert, M. M., Friston, K. J., Dolan, R. J., & Garrido, M. I. (2014). Subcortical amygdala pathways enable rapid face processing. *NeuroImage*, *102*, 309–316.
- George, N., Driver, J., & Dolan, R. J. (2001). Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *NeuroImage*, *13*, 1102–1112.
- Gredeback, G., Johnson, S., & von Hofsten C. (2010). Eye tracking in infancy research. *Developmental Neuropsychology*, *35*, 1–19.
- Hadjikhani, N., Hoge, R., Snyder, J., & de Gelder B. (2008). Pointing with the eyes: The role of gaze in communicating danger. *Brain and Cognition*, *68*, 1–8.
- Haxby, J. V., & Ida Gobbin, M. (2007). The perception of emotion and social cues in faces. *Neuropsychologia*, *45*, 1.
- Haxby, J. V., Hoffman, E. A., & Gobbin, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.
- Haxby, J. V., Hoffman, E. A., & Gobbin, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, *51*, 59–67.
- Helminen, T. M., Kaasinen, S. M., & Hietanen, J. K. (2011). Eye contact and arousal: The effects of stimulus duration. *Biological Psychology*, *88*, 124–130.
- Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience*, *21*, 1229–1243.
- Hoehl, S., & Striano, T. (2010). Infants' neural processing of positive emotion and eye gaze. *Social Neuroscience*, *5*, 30–39.
- Hoehl, S., Reid, V. M., Parise, E., Handl, A., Palumbo, L., & Striano, T. (2009). Looking at eye gaze processing and its neural correlates in infancy—implications for social development and autism spectrum disorder. *Child Development*, *80*, 968–985.
- Ishai, A. (2008). Let's face it: It's a cortical network. *NeuroImage*, *40*, 415–419.
- Itier, R. J., & Batty, M. (2009). Neural bases of eye and gaze processing: The core of social cognition. *Neuroscience and Biobehavioral Reviews*, *33*, 843–863.
- Jasper, H. H., & Andrews, H. L. (1938). Brain potentials and voluntary muscle activity in man. *Journal of Neurophysiology*, *1*, 87–100.
- Jayaraman, S., Fausey, C. M., & Smith, L. B. (2013). Developmental see-saws: Ordered visual input in the first two years of life. In: M. Knauff, M. Pauen, N. Sebanz, & I. Wachsmuth (Eds.), *Proceedings of the 35th Annual Conference of the Cognitive Science Society* (pp. 669–674). Austin, TX: Cognitive Science Society.
- Jayaraman, S., Fausey, C. M., & Smith, L. B. (2015). The faces in infant-perspective scenes change over the first year of life. *PLoS One*, *10*, e0123780.
- Just, M. A., & Carpenter, P. A. (1980). A theory of reading: From eye fixations to comprehension. *Psychological Review*, *87*, 329–354.
- Klein, J. T., Shepherd, S. V., & Platt, M. L. (2009). Social attention and the brain. *Current Biology: CB*, *19*, R958–R962.
- Kleinke, C. L. (1986). Gaze and eye contact: A research review. *Psychological Bulletin*, *100*, 78–100.
- Lachat, F., Hugueville, L., Lemarechal, J. D., Conty, L., & George, N. (2012). Oscillatory brain correlates of live joint attention: A dual-EEG study. *Frontiers in Human Neuroscience*, *6*, 156.
- Land, M. F., & Tatler, B. W. (2009). *Looking and acting: Vision and eye movements in natural behaviour*. Oxford: Oxford University Press.
- Langton, S. R., Watt, R. J., & Bruce, I. I. (2000). Do the eyes have it? Cues to the direction of social attention. *Trends in Cognitive Sciences*, *4*, 50–59.
- Materna, S., Dicke, P. W., & Thier, P. (2008). The posterior superior temporal sulcus is involved in social communication not specific for the eyes. *Neuropsychologia*, *46*, 2759–2765.
- Medaglia, J. D., Lynall, M. E., & Bassett, D. S. (2015). Cognitive network neuroscience. *Journal of Cognitive Neuroscience*, *28*, 1–21.

- Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 1680–1685.
- Mundy, P., Card, J., & Fox, N. (2000). EEG correlates of the development of infant joint attention skills. *Developmental Psychobiology*, *36*, 325–338.
- Musicus, A., Tal, A., & Wansink, B. (2015). Eyes in the aisles: Why is cap’n crunch looking down at my child? *Environment and Behavior*, *47*, 715–733.
- Nelson, C. A. (2001). The development and neural bases of face recognition. *Infant and Child Development*, *10*, 3–18.
- Ninio, A., & Bruner, J. (1978). The achievement and antecedents of labelling. *Journal of Child Language*, *5*, 1–15.
- Parise, E., Reid, V. M., Stets, M., & Striano, T. (2008). Direct eye contact influences the neural processing of objects in 5-month-old infants. *Social Neuroscience*, *3*, 141–150.
- Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, *335*, 23–30.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1989). Positron emission tomographic studies of the processing of single words. *Journal of Cognitive Neuroscience*, *1*, 153–170.
- Ponkanen, L. M., & Hietanen, J. K. (2012). Eye contact with neutral and smiling faces: Effects on autonomic responses and frontal EEG asymmetry. *Frontiers in Human Neuroscience*, *6*, 122.
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience*, *18*, 2188–2199.
- Puce, A., Smith, A., & Allison, T. (2000). ERPs evoked by viewing facial movements. *Cognitive Neuropsychology*, *17*, 221–239.
- Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124*, 372–422.
- Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In: C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV* (pp. 231–265). Cambridge: MIT Press.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research Cognitive Brain Research*, *3*, 131–141.
- Rosati, A. G., & Hare, B. (2009). Looking past the model species: Diversity in gaze-following skills across primates. *Current Opinion in Neurobiology*, *19*, 45–51.
- Rossi, A., Parada, F. J., Kolchinsky, A., & Puce, A. (2014). Neural correlates of apparent motion perception of impoverished facial stimuli: A comparison of ERP and ERSP activity. *NeuroImage*, *98*, 442–459.
- Rossi, A., Parada, F. J., Latinus, M., & Puce, A. (2015). Photographic but not line-drawn faces show early perceptual neural sensitivity to eye gaze direction. *Frontiers in Human Neuroscience*, *9*, 185.
- Scaife, M., & Bruner, J. S. (1975). The capacity for joint visual attention in the infant. *Nature*, *253*, 265–266.
- Schooler, J. W., Smallwood, J., Christoff, K., Handy, T. C., Reichle, E. D., & Sayette, M. A. (2011). Meta-awareness, perceptual decoupling and the wandering mind. *Trends in Cognitive Sciences*, *15*, 319–326.
- Shepherd, S. V. (2010). Following gaze: Gaze-following behavior as a window into social cognition. *Frontiers in Integrative Neuroscience*, *4*, 5.
- Sporns, O., Chialvo, D. R., Kaiser, M., & Hilgetag, C. C. (2004). Organization, development and function of complex brain networks. *Trends in Cognitive Sciences*, *8*, 418–425.
- Sporns, O., Tononi, G., & Kotter, R. (2005). The human connectome: A structural description of the human brain. *PLoS Computational Biology*, *1*, e42.
- Stanley, D. A., & Adolphs, R. (2013). Toward a neural basis for social behavior. *Neuron*, *80*, 816–826.

- Steinhauer, S. R., Siegle, G. J., Condray, R., & Pless, M. (2004). Sympathetic and parasympathetic innervation of pupillary dilation during sustained processing. *International Journal of Psychophysiology*, *52*, 77–86.
- Tanner, J., & Byrne, R. (1993). Concealing facial evidence of mood: Perspective-taking in a captive gorilla? *Journal of Primatology*, *34*, 451–457.
- Thunstrom, M., Kuchenbuch, P., & Young, C. (2014). Concealing of facial expressions by a wild Barbary macaque (*Macaca sylvanus*). *Journal of Primatology*, *55*, 369–375.
- Tomasello, M. (1995). Joint attention as social cognition. In: C. D. Moore & J. Philip (Eds.), *Joint attention: Its origins and role in development* (pp. 103–130). New York: Lawrence Erlbaum Associates Inc.
- Tomasello, M. (2008). *Origins of human communication*. Cambridge: MIT Press.
- Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states—The question is which ones and to what extent. *Trends in Cognitive Sciences*, *7*, 153–156.
- Torralba, A., Oliva, A., Castelhan, M. S., & Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. *Psychological Review*, *113*, 766–786.
- Ulloa, J. L., Puce, A., Hugueville, L., & George, N. (2014). Sustained neural activity to gaze and emotion perception in dynamic social scenes. *Social Cognitive and Affective Neuroscience*, *9*, 350–357.
- Vecera, S. P., & Johnson, M. H. (1995). Gaze detection and the cortical processing of faces: Evidence from infants and adults. *Visual Cognition*, *2*, 59–87.
- Vo, M. L., Smith, T. J., Mital, P. K., & Henderson, J. M. (2012). Do the eyes really have it? Dynamic allocation of attention when viewing moving faces. *Journal of Vision*, *12*, pii: 3.
- de Waal F. (1986). *Chimpanzee politics*. New York: Harper and Row.
- Walter, W. G. (1936). The location of cerebral tumors by electroencephalography. *Lancet*, *2*, 305–308.
- Wieser, M. J., Pauli, P., Alpers, G. W., & Muhlberger, A. (2009). Is eye to eye contact really threatening and avoided in social anxiety?—An eye-tracking and psychophysiology study. *Journal of Anxiety Disorders*, *23*, 93–103.
- Woodward, A. L., & Gerson, S. A. (2014) Mirroring and the development of action understanding. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, *369*, 20130181.
- Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum Press.
- Yoss, R. E., Moyer, N. J., & Hollenhorst, R. W. (1970). Pupil size and spontaneous pupillary waves associated with alertness, drowsiness, and sleep. *Neurology*, *20*, 545–554.
- Zalesky, A., Fornito, A., Cocchi, L., Gollo, L. L., & Breakspear, M. (2014). Time-resolved resting-state brain networks. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 10341–10346.