

A Cognitive Neuroscience View on Pointing: What Is Special About Pointing with the Eyes and Hands?

José Luis Ulloa * † ‡
jose.ulloa_fulgeri@etu.upmc.fr

Nathalie George * † ‡
nathalie.george@upmc.fr

ABSTRACT

When interacting with others, we often use bodily signals to communicate. Among these signals, pointing, whether with the eyes or the hands, allows coordinating our attention with others, and the perception of pointing gestures implicates a range of social cognitive processes. Here, we review the brain mechanisms underpinning the perception and understanding of pointing, focusing on eye gaze perception and associated joint attention processes. We consider pointing gesture perception, but leave aside pointing gesture execution as it relates to a distinct area of cognitive neuroscience research. We describe the attention orienting effects of pointing and the neural substrates for the perception of biological cues. We consider the multiple high-level social cognitive processes elicited by pointing gesture perception and examine how pointing gestures are related to the general taxonomy of gestures. We conclude by emphasizing that pointing is a social phenomenon and that a full account of pointing will require an integrative approach taking into account the distinct perspectives from which this phenomenon can be investigated.

KEYWORDS: Gaze; Pointing; Neuroimaging; Joint attention; Biological cues; Social cognition

* CNRS, UMR 7225, CRICM, Paris, France

† Inserm, U 975, Paris, France.

‡ Université Pierre et Marie Curie-Paris 6, Centre de Recherche de l'Institut du Cerveau et de la Moelle Epinière (CRICM), UMR_S 975, and Centre MEG - CENIR, Paris, France.

Introduction

In cognitive neuroscience, social cognition refers to the processing of information related to conspecifics. It encompasses an array of different but overlapping cognitive processes, among which social attention appears as a linchpin phenomenon. The study of social attention has benefited from the junction of distinct disciplines and from the recent advances in brain imaging. Here, we will review distinctive neurocognitive aspects of social attention. Most of this research has focused on *eye gaze perception*, viz. *pointing with the eyes*. However, *pointing gestures*, e.g. *pointing with the hands*, are equally important and will also be considered. Social attention involves multiple, intimately intricated, cognitive processes. The current approach has examined these processes separately, but efforts are now taking place to conceive a more realistic model that considers the complexity and richness of social behavior. The first section describes the attention orienting effects of eye gaze and pointing gestures perception. Next, we review some evidence of brain systems dedicated to the perceptual analysis of biological cues. Finally, we describe high-level socio-cognitive processes, such as joint attention, associated with pointing gesture processing, and we relate pointing to gesture comprehension. We conclude that the cognitive neuroscience approach must be tied together with other disciplinary approaches in order to give a full account of pointing as a social phenomenon.

1. Attentional effects of eye gaze and pointing gestures

Behavioral aspects of attention orienting

Attention orienting entails selectively allocating cognitive resources to detect and process a given aspect of the environment. Current neurocognitive models suggest that different types of attention involve distinct, although overlapping, brain regions. These models distinguish top-down processes that are driven by knowledge, expectations, and goals, from bottom-up processes that are driven mainly by the properties of the stimulus and its sensory context. Top-down factors are held to elicit endogenous (or voluntary) attention because they imply knowledge activation to elicit attention orienting (e.g. orienting to arrows implies – in principle – knowing the symbolic, directional meaning of arrows). By contrast, attention orienting induced by the sensory properties of stimuli (e.g. a sudden peripheral flash of light) are said to be exogenous (or

reflexive) and to be related to bottom-up processing (for reviews see Corbetta et al., 2002; Raz & Buhle, 2006).

When interacting with others we automatically detect and almost systematically follow their focus of attention (Frischen et al., 2007, Klein et al., 2009; Nummenmaa et al., 2009). Attention orienting elicited by the perception of others' attentional focus has been studied using faces as cues to orient an observer's attention in variations of the classical attention cueing paradigm of Posner (1980). Typically, a face cue with its eyes directed to one side of the display is presented centrally. A target requiring a speeded response then appears to the left or right side of the display. Targets items elicit more rapid responses when they appear in a location congruent with the direction of the eye gaze rather than in the opposite location. This occurs even when eye gaze direction is unpredictable (Friesen & Kingstone, 1998) or counterpredictive (Driver et al., 1999; Downing et al., 2004; Friesen et al., 2004) of target location, thus disclosing its reflexive nature. However, this attentional effect is not purely exogenous. Indeed, exogenous attention orienting is usually associated with an "inhibition of return" (IOR) effect: When the time interval between the cue and the target stimulus (*viz.* the stimulus-onset asynchrony, SOA) exceeds a few hundreds of milliseconds, the responses to the congruent targets become slower (instead of faster) than those to the incongruent targets, reflecting a sort of refractory period of attention at the previously cued location, which is known as the IOR effect and considered as a hallmark of exogenous attention. The IOR effect was not found following attention orienting by eye gaze (Friesen & Kingstone, 1998; Driver et al., 1999; Frischen & Tipper, 2004) and some studies demonstrated independent and co-occurring effects of attention orienting by eye gaze and IOR (Friesen & Kingstone, 2003). These findings suggest that eye gaze does not elicit a typical exogenous orienting effect.

Moreover, the contribution of endogenous attention to the orienting effect elicited by eye gaze has been investigated by comparing eye gaze cues and symbolic cues such as arrows. Although there is some evidence that arrows may elicit some form of reflexive orienting (Muller & Rabbitt, 1989; Tipples, 2002), this latter type of cues is held to elicit mostly endogenous orienting. Indeed, insofar as a symbol is something that represents or stands for something else – usually by convention or association (Mehu et al., 2012), decoding the directional meaning of an arrow relies on previous knowledge of what it represents. When the orienting effects of arrows and eye gaze are put

into competition with voluntary orienting, orienting to arrows is abolished whereas orienting to eye gaze direction persists (Friesen et al., 2004). This study also showed that both voluntary attention and orienting to eye gaze can co-occur, suggesting that attention orienting triggered by eye gaze may not be simply an over-learned form of voluntary orienting either.

In sum, the available evidence suggests that attention orienting associated with eye gaze perception may be subtended by a distinct system from that subserving endogenous and exogenous attention, thus emphasizing the singular nature of the attentional processes elicited by perceiving eye gaze.

Gestures are another important source of attentional information from others (Kendon, 1994). Some authors suggest that understanding pointing gestures may require cognitive developmental changes related to the understanding of symbols (Butterworth, 1995), for instance, changes in representational thinking (see De Loache, 1991). This will be further developed later. If pointing gestures require symbolic decoding, they should elicit different attention orienting effects in comparison to eye gaze because additional stages of processing are involved. However, pointing gestures elicit rapid attention orienting similar to that triggered by eye gaze (Fischer & Szymkowiak, 2004; Belopolsky et al., 2008; Sato et al., 2009). Furthermore, interference studies have shown that pointing gestures and eye gaze share some attentional properties. There are mutual interference effects elicited by the perception of pointing gestures and of eyes/head gaze orientations on the processing of directionality (Langton & Bruce, 2000). However, it has been shown that at least some pointing gestures, such as thumb gestures, may not bear an intrinsic directional meaning. When participants are asked to categorize thumb gestures as thumbs-up or thumbs-down, there is no interference of the gaze orientation (conveyed by the eyes and head) on the requested categorization; this suggests that gaze orientations and thumb gestures bear independent meanings, the former being intrinsically directional while the latter is dependent on task demands (Langton & Bruce 2000). This suggests that pointing gestures can elicit fast attention orienting effects but these are dependent on the interpretation of these gestures as directional.

Overall, the attention orienting effect elicited by pointing gestures do not seem as 'irrepressible' as the one elicited by eye gaze although additional studies are required to further clarify the differences between the attentional effects of eye gaze and pointing gestures.

Neural aspects of attention orienting

Current neurocognitive models state that attention is underpinned by the dynamic interaction of two partially segregated brain systems: One system is centered on the dorsal posterior parietal and frontal cortices; it involves the selection of sensory information and responses, thus underpinning endogenous attention processes. The other system is largely lateralized to the right hemisphere and centered on the temporo-parietal and ventral frontal cortices; it is recruited during the detection of behaviorally relevant sensory events, particularly when they are salient and unattended; it is thus involved in exogenous attention (for a review see Corbetta et al., 2000). Exogenous orienting also implicates a mesencephalic structure of the brain, the superior colliculus, that may be responsible for the IOR effect (e.g. Sapir et al., 1999).

Attention orienting elicited by eye gaze involves an extensive brain network encompassing the endogenous and the exogenous systems, with the respective contribution of each system still to be clarified. The absence of gaze cueing effects in patients with frontal lobe damage (Vecera & Rizzo, 2004) and brain imaging studies (e.g. Nummenmaa et al., 2010) suggest that voluntary attention contributes to the attention orienting triggered by eye gaze. Yet, the attentional effects of gaze seem to be rooted in a different neural organization from that subtending endogenous orienting by symbolic cues. Eye gaze perception activates a more reflexive attentional system than the one activated by arrow perception (Hietanen et al., 2006, 2008; Engell et al., 2010). Furthermore, it has been shown that orienting by eye gaze and exogenous orienting engage similar cortical mechanisms (Greene et al., 2009). On the other hand, neuropsychological studies have shown that reflexive orienting induced by eye gaze shift depend more on cortical than subcortical mechanisms (Kingstone et al., 2000; Ristic et al., 2002), thus suggesting that eye gaze perception activates an atypical type of exogenous attention system. In sum, although this needs confirmation, it seems that the specificity of attention orienting effects induced by eye gaze perception may lie in the relative strength with which the endogenous (Tipper et al., 2008; Brignani et al., 2009) and exogenous attention (Nagata et al., 2012) networks are engaged.

Attention orienting by eye gaze selectively activates the superior temporal sulcus (STS), a major sulcal landmark in the temporal lobe (Kingstone *et al.*, 2004). This structure may be involved in the processing of biological information (see section 2). Both eye gaze and pointing gestures elicit

activation in the STS when they are perceived as directional cues (Materna et al., 2008). Furthermore, the perception of eye gaze, arrows and pointing gestures compared to their non-directional counterparts, elicits similar cortical activations (Sato et al., 2009). In this study, STS activation was, however, less robust for pointing gestures than for eyes and arrows. Event related-potential (ERP) studies show similarities in the neural architecture subtending the attentional effects of eye gaze and pointing gestures. The ERP patterns associated with congruent and incongruent pointing gesture and eye gaze cues are closely similar, and they may involve the STS (Gredebäck & Melinder, 2010). Conversely, there is also evidence that suggest there are distinct neural substrates for eye gaze and pointing gesture processing. For instance, a repetition-suppression paradigm demonstrated that responses to eye gaze shifts could not be suppressed by pointing gestures (Bayliss et al., 2011), suggesting that attentional changes induced by pointing gestures were not able to modify the neural responses to eye gaze. Thus, although the directional processing of pointing gestures and eye gaze relies on a partly common neural network, involving in particular the STS (Puce & Perrett, 2003), there seems to be some neural specificity of attentional processes associated with eye gaze (Wheaton et al., 2004).

It is conceivable that social attentional processing relies not only on a specialized attentional system, but also on general attentional mechanisms that receives particularly rapid or dominant inputs from sensory regions processing social (as compared to non-social) signals (see Heyes, 2003 for an analogous view). Our exquisite sensitivity to signals from others seems to be reflected by the activation of specific brain regions at the very early stages of processing. In other terms, the specificity of pointing may originate from the involvement of specific brain regions attuned to detect biological cues.

2. Visual processing of eye gaze and pointing gestures

In the early neuroscientific era, researchers evaluated the neural responses to visual stimulations with the idea that if neurons responded selectively to certain categories of visual stimuli, then they should represent something of the perceptual categorical meaning of these stimuli. In the 60's and 70's, seminal studies of Charles Gross and colleagues described cortical cells selectively activated by faces and hands (Gross et al., 1969, 1972), supporting the concept of 'the grandmother cell' – a neuron (or a small group of neurons)

responding only to a specific, complex, and meaningful stimulus (Gross, 2002). The idea that perceptual experience could be rooted in the activity of such small neuronal assemblies has been fairly criticized. However, current evidence supports the notion that some specialized brain regions play a major role and may contribute directly to the meaningful experience of perception. Abundant evidence from human brain lesion data, non-human primate data as well as brain imaging indicates that the human brain is particularly sensitive to biological cues such as the human body and its parts.

An ongoing debate in neuroscience is whether the brain represents and processes information in a modular or in a distributed fashion. Many studies seem to indicate there is visual brain specialization for specific categories of stimuli. A circumscribed region in the visual occipital lobe has been identified as responding selectively to the sight of bodies or body parts (Downing et al., 2001; Grossman & Blake, 2002). The so-called extrastriate body area (EBA) seems to be responsible for the identification of other people's bodies, and it also allows perceiving the position of one's own body during the guidance of action; it has been related to planning, executing, and imagining one's own movements (Astafiev et al., 2004). Additional evidence in favor of a modular theory of brain functioning comes from studies on the fusiform gyrus (FG), a ridge on the inferior surface of the temporal lobe. A sub-region of the FG has been called the fusiform face area (FFA) because it is consistently activated during face perception; the FFA would particularly be involved in the perception of the invariant aspects of faces (Hoffman & Haxby, 2000; Haxby et al., 2002). Furthermore, lesions to the FFA can be associated with deficits of face recognition (e.g. Meadows, 1974).

The implication of visual brain regions such as the EBA and the FFA should however be interpreted with caution. These regions could constitute one component of a larger set of brain regions attuned to process social signals. For instance, the STS is the putative host for many cognitive functions ranging from speech perception to social attention. STS responds to biological motion (for a review see Allison et al., 2000) including eye gaze, hand movements, and gestures (Bonda et al., 1996; Calder *et al.*, 2007; Grèzes et al., 1999; Nakamura et al., 2004; Thompson et al., 2007). Yet, its functions are known to go beyond biological cue detection, because STS is sensitive to contextual information. STS cells in monkeys respond to the sight of reaching actions only when the agent performing the action is seen to attend the target position of the action (Jellema et al., 2000). Similarly, STS responses to eye gaze are

modulated if eye gaze is directed toward an object (Pelphrey et al., 2003). Thus, in concert with other brain regions, the STS may integrate multiple information allowing decoding the meaning of biological cues (Hein & Knight, 2008). Another key structure involved in the processing of social information is the amygdala. This complex of nuclei located in the anterior part of the medial temporal lobe has been associated with socio-emotional processing (LeDoux, 2000; Adolphs, 2010), including face and eye gaze perception (George et al., 2001), and it has been more generally involved in relevance appraisal processes (Sander et al., 2003; Ousdal et al., 2008). The multiple functions of the amygdala can be directly related to its extensive connectivity with numerous other brain regions (Pessoa & Adolphs, 2010). Overall, it seems that the brain regions crucial to social perception owe their functionality and versatility to their broad connectivity with other regions as well as to some degree of functional specialization.

How is the visual processing of eye gaze and pointing gestures related to the other types of processes elicited by these stimuli? In particular, how is it related to the social cognitive processes elicited by the perception of eye gaze and pointing gestures such as attention orienting, joint attention and social coordination? The human brain is exquisitely sensitive to social cues and there is convincing evidence that the processing of these cues involves a distinctive pattern of brain activity in a set of specific, distributed regions, already from initial perceptual analysis stages. These regions would feed into later stages of processing and contribute directly to the understanding of social signals. Furthermore, present neurocognitive models acknowledge that perceptual and interpretative (*viz.* meaning decoding) stages of stimulus processing are tightly interrelated and hardly dissociable (Hochstein and Ahissar, 2002; Kveraga et al., 2007).

3. Social processing of eye gaze and pointing gestures

Sensitivity to social cues seems to be present from birth in human beings (Farroni et al., 2000), but many skills associated with the processing of these cues are acquired through experience, as can be seen by the developmental trajectory of eye gaze perception, from gaze contact and mere gaze following to sophisticated social understanding (Emery, 2000). Humans are experts at interpreting signals from their conspecifics. To interpret and make sense of these signals entails to interpret gestures as produced by minded agents, *i.e.* by

individuals that can feel and act according to their own thoughts (Waytz et al., 2010). Thus, seeing eye gaze and pointing gestures not only involves attentional orienting, it also prompts further high-level social cognitive processes engaging people into a dynamic and coordinated inter-action that allow making sense of others.

What are the social cognitive processes involved in eye gaze and pointing gesture processing? We will not attempt to provide an exhaustive list of these processes here, but rather underline some of these processes that are relevant to the understanding of pointing. Making sense of others means to be able to explain and predict others' behaviors. The ability to attribute mental states has been termed "theory of mind" (ToM), which postulates that we formulate a psychological theory of the mental states of others (Fodor, 1992). Distinct regions of the prefrontal cortex (PFC) seem to subtend different functions in relation with mindreading. The ventromedial PFC has been proposed to play a role in the decoding of the affective meaning of sensory stimuli (Grossman et al., 2010; Roy et al., 2012), indicating some common neural substrates for mindreading and affective processing. The dorsomedial PFC is engaged when a subject experiences the sense of self, thus allowing self/other distinctions and enabling the understanding of triadic relationships between the self, other agents, and external objects (Schilbach et al., 2006), as typically instantiated in pointing. In addition, the processing of the self, as elicited by calling a subject's own name or by gazing directly at the subject, elicits changes in frontal as well as parietal brain areas (Kampe et al., 2003). The activation of the temporo-parietal junction (TPJ) has been associated with the sense of agency, or the capacity to experience the self as the cause of an external or a sensory event. TPJ is also associated with theory of mind, empathy, and attentional orienting (Decety & Lamm, 2007), emphasizing the tight links between these processes.

Intention attribution, an aspect of mindreading, may be also important to make sense of pointing. Motion is a key attribute that evokes the ascription of intentions. For instance, participants attribute mental states to simple geometric shapes on the basis of their observed characteristic movements (Heider & Simmel, 1944). This mental state attribution is associated with activity in frontal brain areas (Castelli et al., 2000). This tendency to attribute intentions to animated agents may explain the involvement of intention attribution during the perception of pointing gestures and eye gaze. Moreover, understanding pointing (with the eyes or the hand) implicates the

understanding of actions, an intense topic of study within social cognitive neuroscience. Action understanding is essential to coordinate our actions with others. Some authors have proposed that a direct link between observing others' actions and ascribing mental states may exist. A simulationist hypothesis of social cognition argues that the understanding of others could involve simulating others' mental states. The discovery of 'mirror neurons' that respond to performing as well as to observing others' actions (e.g. di Pellegrino et al., 1992, Rizzolati et al., 1996) has led to the hypothesis that simulating others' mental states would be done through the motor neural system (Gallese & Goldman, 1998). The precise mechanism by which the mirror system may contribute to social processing has not been fully clarified and its role continues to be highly debated (e.g. Jacob, 2008; Goldman, 2009). Yet, it is interesting to note that mirror mechanisms have been proposed as general mechanisms for the understanding of others. Furthermore, Shepherd and cols (2009) recently reported the existence of gaze mirror neurons in monkeys. They proposed that these neurons could directly contribute to gaze following behavior and that they may participate in attention mirroring mechanisms that would be involved in joint attention.

All the processes mentioned above contribute in concert to making sense of others. Consequently, they are involved to some degree in making sense of others' eye gaze and pointing gestures. Further research is however needed to know precisely how processes like the self, mindreading, inference of others' actions, and intention attribution contribute to decode the meaning of pointing gestures.

4. Specific aspects of eye gaze versus other pointing gestures

Making sense of eye gaze and pointing gestures implies understanding the referential nature of these cues. Eye gaze and pointing gestures may not bear an intrinsic meaning; rather they serve to orient the perceiver's attention to specific contextual information (Tomasello, 1995). Rather than being encoded in the signal, the relevant information has to be inferred by the perceiver from contextual cues and from shared knowledge about the context (Mehu et al., 2012). Both eye gaze and pointing gestures may bring something to notice, but an important difference between these two types of pointing cues is that the referential function of the eyes arises as a secondary consequence of the primary function of seeing. We look at objects, persons, or locations when we

are planning to perform actions in the corresponding direction or because our attention has been attracted toward these stimuli. Moving our eyes primarily allows us to see, whether in solitude or in the presence of others. In the latter case, eye gaze reveals to the fellow observers our attentional focus even if we are not willing to do so. Thus, our eye movements convey meaningful information about the environment and ourselves, even if they are not intentionally communicative.

Furthermore, eye gaze perception is intrinsically and strongly associated to facial expression perception. Many studies show the mutual influence of eye gaze and emotion perception at behavioral (Adams et al., 2003; Sander et al., 2007, see Graham and Labar, 2012 for a review) and neural levels (Hietanen et al., 2008b; Hadjikhani et al., 2008; N'Diaye et al., 2009; Ulloa et al., in press). It is perhaps as a result of this mutual influence that eye gaze perception is frequently - if not systematically - ascribed with affective meaning. An interesting consequence of the affective ascription to eye gaze is that affective valuations spread from the gazer to the observer. It has been shown that objects that are looked-at by someone else are preferred relative to objects that are not looked at by others (Bayliss et al., 2006). This suggests that not only we tend to ascribe affective meaning to the gaze of others, we also tend to mimic what we interpret as affective attributions of others. Linking a social partner and the target of his/her attention in this way means to conceive eye gaze as an intentional device, representing a basic level of social attention conveyed by the eyes (Shepherd & Cappuccio, 2011), which may be specific to eye gaze as compared to other types of pointing phenomena.

Eye perception may also be essential to the understanding of pointing gestures. Contextual information associated to pointing gestures incorporates eye gaze information in the form of eye contact. We may thus consider the perception of eye gaze as bearing two aspects: there is a natural tendency to attribute meaning to eye movements (as detailed above), and there is a communicative stance engendered by eye contact (Kleinke, 1986; George & Conty; Senju & Johnson, 2009). In human interactions, eye contact signals an explicit communicative intention to the beholder and sets up a common social ground of shared intentionality, i.e. the intention to share a mental state (Tomasello & Carpenter, 2007). Eye contact is highly salient and triggers differentiated neurocognitive effects relative to other gaze directions (Conty et al., 2010a, b), perhaps enabling its communicative function. Pointing gestures have a clear intentional communicative dimension insofar as they are displayed

in explicit communicative contexts. This communicative context is established by an indicator of communicative intent: a verbal cue or eye contact (Emery, 2000). Thus, the occurrence of eye contact sets the communicative stance of behaviors involving eye gaze and pointing gestures.

Moreover, the combination of eye contact with gaze following provides the basis for joint attention. Joint attention is the shared focus of attention of two individuals onto an object; it is achieved when one individual signals an object to another individual by means of eye gaze and/or pointing gestures. Joint attention is more than a geometric phenomenon of visual attention alignment, because it requires that the individuals know that they are attending to something in common (Tomasello, 1999). Former studies, as detailed above, have examined the perception of eye gaze and highlighted its attentional effects. Subsequent studies have shown that following others' eyes elicit brain activity related to mindreading (Calder et al., 2002; Williams et al., 2005; Conty et al., 2007). Further steps are now being undertaken by developing paradigms that approach real-life situations of dynamic interactions. Recent studies show that joint attention involves extensive activation of the attentional, mindreading (Saito et al., 2010; Redcay et al., 2012) and reward-related (Schilbach et al., 2010) brain systems. Recently, a study using a real-life face-to-face paradigm revealed the contributions of mutual attentiveness, attention mirroring, and inter-personal coordination to joint attention (Lachat et al., 2012). In sum, through joint attention mechanisms, eye gaze perception activates rich social cognitive processes.

Pointing gestures have perceptive and attentional features that have been partly identified. The study of pointing gestures needs to be undertaken in the context of real-life human interactions, but to date, there is no study combining joint attention paradigms with pointing gestures. Just recently, some incipient studies have attempted at setting up ecologically valid paradigms by manipulating eye gaze and pointing gestures together. For instance, Conty et al. (2012) investigated the integration of directional cues from gaze, conveyed by eye and head orientation, and pointing gestures, revealing the involvement of brain regions associated to attention and motor processing in the early stages of the processing of these cues.

5. The processing of gestures

To capture the meaning of pointing gestures we may distinguish distinct levels of intentions in the individual performing the pointing (*viz.* the pointer) (Tomasello et al., 2007). These distinct levels of intentions constitute the context wherein the pointing gesture is deployed and any model of pointing should aim at understanding how they contribute to decode the meaning of a pointing gesture. Among contextual elements, the communicative intentional stance is often, but not exclusively, conveyed by eye contact. Another important element is the social – or interpersonal – intention. The motive of directing someone’s attention toward some particular location can be informative, requestive or expressive (see Tomasello et al., 2007 for more details). The social intention behind a pointing gesture is often associated to some form of emotional facial expression present in the pointer, thus involving emotion-related neural systems (a description of these systems can be found elsewhere; see e.g., George, 2013). This converges with the notion that joint attention is intimately linked to emotion processing (Schilbach et al., *in press*). Furthermore, what is most immediately grasped by a beholder is the referential intention, which is the first and necessary step to decode the meaning of a pointing gesture. As detailed above, the neural substrates subtending the decoding of the referential information associated with eye gaze are known to involve an extended perceptual and attentional network.

Understanding pointing gestures may require some sort of symbolic decoding. Pointing gestures are stimuli (e.g. a hand) that stand for something else, namely a direction or point in the surrounding space. By contrast, eye gaze may be considered as holding a more ‘natural’ meaning because its significance is not explicitly learned, rather, it is directly perceived: When a person directs his/her eyes toward an object, this behavior becomes directly significant for an observer, allowing this observer to ponder putative underlying motives on the basis of such behavior. Such intentional states are not re-presented elsewhere, because there is no distinction between what represents and what is represented. The intentions expressed by the interactants are directly recognized and mapped by the beholder in terms of his/her own bodily dispositions. This perception is direct and does not require a symbolic model (Cappuccio & Wheeler, 2011). In other terms, the eyes do not stand for a direction or point in the surrounding space, rather they induce attentional changes in the beholder. This behavior may be implicitly learned

during ontogeny as humans learn that the eyes are useful to predict others' behavior and then equate eye movements to intentions and goals (Tomasello et al., 2005). In contrast, pointing gestures are conventionalized and culturally standardized symbols that are representative in nature because their meaning go beyond their physical nature. To what extent, embodied and representative dimensions of pointing gestures contribute to the understanding of these gestures by beholders is an intriguing and stimulating, yet unexplored, issue in neuroscience. The study of the neural substrates of gesture comprehension has just recently begun and it might encourage the inquiry about pointing gestures.

There are different types of manual gestures. Deictic gestures draw attention to something in the environment. Conventional gestures or emblems use a standardized form to convey a culturally specific meaning. Representational gestures capture aspects of an action, object, or idea either iconically as in pantomimes or metaphorically as in gesticulations representing abstract ideas (for a review, see Cartmill et al., 2012). Deictic gestures do not bear an intrinsic meaning like conventional or representational gestures do. Instead, the function of deictic gestures is to orient attention. In this sense, the meaning of pointing gestures is more pragmatic than the meaning of other gestures. Another type of manual gestures is the sign language, a codified system in which hand signs are used to communicate. According to the Kendon's continuum (McNeill, 1992) there is a decreasing presence of speech and an increase in language-like features from gesticulations to pantomimes, to emblems, and to sign languages. The first type of gestures could be sought as manual movements with an abstract meaning that depends heavily on speech to make sense whereas the last type represent movements with more concrete meaning that could dispense from speech since they themselves possess a language structure. Brain mechanisms coding gestures might rely more on the brain systems for action with regard to the first type of gestures and more on the brain systems for language with regard to the last type of gestures.

A strong and recurrent relationship between gestures and action has been shown. This relationship seems to concern mostly representational gestures, since they can be regarded as a type of simulated action. Accordingly, these types of gesture have been associated to activity in the mirror neuron system (for reviews see Cartmill et al., 2012; Willems & Hagoort, 2007). On the other extreme, the perception of sign language has been consistently reported to elicit activity in perisylvian regions such as the inferior frontal gyrus and

posterior temporal cortices that belong to the classical language network (Willems & Hagoort, 2007). For example, the perception of emblems has been related to neurophysiological markers of lexical-semantic processing (Gunter & Bach, 2004). Interestingly, even gestures approaching the ‘action’ side of the gesture spectrum, such as pantomimes and emblems, activate the perisylvian network, when compared to spoken words (Xu et al., 2009). In another study, brain activity was investigated for the perception of emblematic and deictic gestures as compared to linguistic stimuli – viz. words; every type of stimuli were presented in a communicational context and compared to their non-communicative counterparts (Enrici et al., 2011). Linguistic stimuli were shown to recruit a perisylvian network while gestures seemed to recruit a sensorimotor network, and both linguistic stimuli and gestures activated an intention processing network. It is important to note that Broca’s area and the putative mirror neuron system in humans are both located in the inferior frontal gyrus. So, although subserving language, this region is also associated to action observation, and to other putative functions such as hierarchical processing (e.g. Koechlin & Jubault, 2006). In this respect, it is not surprising that language and action recruit some overlapping parts of the brain. Some authors have even proposed that the information that characterizes conceptual knowledge is available at neural level in the sensorimotor system (Tettamanti et al., 2005; Gallese & Lakoff, 2005).

Gesture comprehension cuts across distinct cognitive domains. Pointing gestures seem to occupy a privileged position in this gesture spectrum because they have a conventional deictic meaning, which, as described before, depends crucially on joint attention. Further studies should provide a framework to combine the study of gestures and joint attention.

Conclusions

The neurocognitive account of pointing is still in progress. Here, we have examined commonalities and differences between eye gaze and pointing gestures. These biological signals elicit attentional changes in the beholder, and they distinctively engage an extended socio-cognitive brain network. The understanding of pointing gestures is intimately linked to eye perception. In order to clarify how pointing gestures are perceived and understood, efforts should be made to bring together the knowledge about gestures and social cognition. Furthermore, the neurocognitive models of pointing should benefit

from the current tendency in social neuroscience to move toward integrative and dynamic approaches of social behavior in close-to-real-life situations.

REFERENCES

- Adams, R.B., Gordon, H.L., Baird, A.A., Ambady, N. and Kleck, R.E. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science* 300, 1536–1536.
- Adolphs, R. (2010). What does the amygdala contribute to social cognition? *Annals of the New York Academy of Sciences* 1191, 42–61.
- Allison T., Puce A. and McCarthy G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences* 4, 267–278.
- Astafiev, S.V., Stanley, C.M., Shulman, G.L. and Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience* 7, 542–548.
- Bayliss, A.P., Bartlett, J., Naughtin, C.K. and Kritikos, A. (2011). A direct link between gaze perception and social attention. *Journal of Experimental Psychology. Human Perception and Performance* 37, 634–644.
- Bayliss, A.P., Paul, M.A., Cannon, P.R. and Tipper, S.P. (2006). Gaze cuing and affective judgments of objects: I like what you look at. *Psychonomic Bulletin & Review* 13, 1061–1066.
- Belopolsky, A.V., Olivers, C.N.L. and Theeuwes, J. (2008). To point a finger: attentional and motor consequences of observing pointing movements. *Acta Psychologica* 128, 56–62.
- Bonda, E., Petrides, M., Ostry, D. and Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *The Journal of Neuroscience* 16, 3737–3744.
- Brignani, D., Guzzon, D., Marzi, C.A. and Miniussi, C. (2009). Attentional orienting induced by arrows and eye-gaze compared with an endogenous cue. *Neuropsychologia* 47, 370–381.
- Butterworth, G. (1995). Origins of mind in perception and action. In: *Joint attention: Its origins and role in development*. Hillsdale, NJ, England: Lawrence Erlbaum Associates. Moore, Chris ; Dunham, Philip J., pp 29–40.

- Calder, A.J., Beaver, J.D., Winston, J.S., Dolan, R.J., Jenkins, R., Eger, E. and Henson, R.N.A. (2007). Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Current Biology* 17, 20–25.
- Calder, A.J., Lawrence, A.D., Keane, J., Scott, S.K., Owen, A.M., Christoffels, I. and Young, A.W. (2002). Reading the mind from eye gaze. *Neuropsychologia* 40, 1129–1138.
- Cappuccio, M. and Wheeler, M. (2011). The sign of the hand: Symbolic practices and the extended mind. *Versus*, 33–56.
- Cartmill, E.A., Beilock, S. and Goldin-Meadow, S. (2012). A word in the hand: action, gesture and mental representation in humans and non-human primates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 367, 129–143.
- Castelli, F., Happé, F., Frith, U. and Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage* 12, 314–325.
- Conty, L., Dezeache, G., Hugueville, L. and Grèzes, J. (2012). Early binding of gaze, gesture, and emotion: neural time course and correlates. *The Journal of Neuroscience* 32, 4531–4539.
- Conty, L., Gimmig, D., Belletier, C., George, N. and Huguet, P. (2010a). The cost of being watched: Stroop interference increases under concomitant eye contact. *Cognition* 115, 133–139.
- Conty, L., N'Diaye, K., Tijus, C. and George, N. (2007). When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. *Neuropsychologia* 45, 3024–3037.
- Conty, L., Russo, M., Lochr, V., Hugueville L., Barbu S., Huguet P., Tijus C., George N. (2010b). The mere perception of eye contact increases arousal during a word-spelling task. *Social Neuroscience* 5, 171–186.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P. and Shulman, G.L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience* 3, 292–297.

- Decety, J. and Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The Neuroscientist* 13, 580–593.
- DeLoache, J.S. (1991). Symbolic functioning in very young children: understanding of pictures and models. *Child Development* 62, 736–752.
- Downing, P., Dodds, C. and Bray, D. (2004). Why does the gaze of others direct visual attention? *Visual Cognition* 11, 71–79.
- Downing, P.E., Jiang, Y., Shuman, M. and Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science* 293, 2470–2473.
- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E. and Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition* 6, 509–540.
- Emery, N.J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews* 24, 581–604.
- Engell, A.D., Nummenmaa, L., Oosterhof, N.N., Henson, R.N., Haxby, J.V. and Calder, A.J. (2010). Differential activation of frontoparietal attention networks by social and symbolic spatial cues. *Social Cognitive and Affective Neuroscience* 5, 432–440.
- Enrici, I., Adenzato, M., Cappa, S., Bara, B.G. and Tettamanti, M. (2011). Intention processing in communication: a common brain network for language and gestures. *Journal of Cognitive Neuroscience* 23, 2415–2431.
- Farroni, T., Johnson, M.H., Brockbank, M. and Simion, F. (2000). Infants' use of gaze direction to cue attention: The importance of perceived motion. *Visual Cognition* 7, 705–718.
- Fischer, M.H. and Szymkowiak, A. (2004). Joint attention for pointing but not grasping postures. *Cortex* 40, 168–170.
- Fodor, J.A. (1992). A theory of the child's theory of mind. *Cognition* 44, 283–296.
- Friesen, C. and Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review* 5, 490–495.
- Friesen, C.K. and Kingstone, A. (2003). Abrupt onsets and gaze direction cues trigger independent reflexive attentional effects. *Cognition* 87, B1–10.

- Friesen, C.K., Ristic, J. and Kingstone, A. (2004). Attentional effects of counterpredictive gaze and arrow cues. *Journal of Experimental Psychology. Human Perception and Performance* 30, 319–329.
- Frischen, A., Bayliss, A.P. and Tipper, S.P. (2007). Gaze cueing of attention: visual attention, social cognition, and individual differences. *Psychological Bulletin* 133, 694–724.
- Frischen, A. and Tipper, S.P. (2004) Orienting attention via observed gaze shift evokes longer term inhibitory effects: implications for social interactions, attention, and memory. *Journal of Experimental Psychology. General* 133, 516–533.
- Gallese, V. and Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences* 2, 493–501.
- Gallese, V. and Lakoff, G. (2005). The Brain's concepts: the role of the Sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology* 22, 455–479.
- George, N. (2013). 7. The facial expression of emotion. In: *The Cambridge Handbook of Human Affective Neuroscience*. Vuilleumier, P. & Armony, J. Cambridge University Press.
- George, N. and Conty, L. (2008). Facing the gaze of others. *Clinical neurophysiology* 38, 197–207.
- George, N., Driver, J. and Dolan, R.J. (2001). Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *NeuroImage* 13, 1102–1112.
- Goldman, A.I. (2009). Mirroring, simulating and mindreading. *Mind & Language* 24, 235–252.
- Graham, R. and Labar, K.S. (2012). Neurocognitive mechanisms of gaze-expression interactions in face processing and social attention. *Neuropsychologia* 50, 553–566.
- Gredebäck, G. and Melinder, A. (2010). The development and neural basis of pointing comprehension. *Social Neuroscience* 5, 441–450.
- Greene, D.J., Mooshagian, E., Kaplan, J.T., Zaidel, E. and Iacoboni, M. (2009). The neural correlates of social attention: automatic orienting to social and nonsocial cues. *Psychological Research* 73, 499–511.

- Grèzes, J., Costes, N. and Decety, J. (1999). The effects of learning and intention on the neural network involved in the perception of meaningless actions. *Brain* 122 (Pt 10)., 1875–1887.
- Gross, C.G. (2002). Genealogy of the “grandmother cell”. *The Neuroscientist* 8, 512–518.
- Gross, C.G., Bender, D.B. and Rocha-Miranda, C.E. (1969). Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science* 166, 1303–1306.
- Gross, C.G., Rocha-Miranda, C.E. and Bender, D.B. (1972). Visual properties of neurons in inferotemporal cortex of the Macaque. *Journal of Neurophysiology* 35, 96–111.
- Grossman, E.D. and Blake, R. (2002) Brain areas active during visual perception of biological motion. *Neuron* 35, 1167–1175.
- Grossman, M., Eslinger, P.J., Troiani, V., Anderson C., Avants B., Gee J.C., McMillan C., Massimo L., Khan A., Antani S. (2010). The role of ventral medial prefrontal cortex in social decisions: converging evidence from fMRI and frontotemporal lobar degeneration. *Neuropsychologia* 48, 3505–3512.
- Gunter, T.C. and Bach, P. (2004). Communicating hands: ERPs elicited by meaningful symbolic hand postures. *Neuroscience Letters* 372, 52–56.
- Hadjikhani, N., Hoge, R., Snyder, J. and De Gelder, B. (2008). Pointing with the eyes: The role of gaze in communicating danger. *Brain and Cognition* 68, 1–8.
- Haxby, J.V., Hoffman, E.A. and Gobbini, M.I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry* 51, 59–67.
- Heider, F. and Simmel, M. (1944). An Experimental Study of Apparent Behavior. *The American Journal of Psychology* 57, 243.
- Hein, G. and Knight, R.T. (2008). Superior temporal sulcus—It’s my area: or is it? *Journal of Cognitive Neuroscience* 20, 2125–2136.
- Heyes, C. (2003) Four routes of cognitive evolution. *Psychological Review* 110, 713–727.
- Hietanen, J.K., Leppänen, J.M., Nummenmaa, L. and Astikainen, P. (2008a) Visuospatial attention shifts by gaze and arrow cues: an ERP study. *Brain Research* 1215, 123–136.

- Hietanen, J.K., Leppänen, J.M., Peltola, M.J., Linna-aho, K. and Ruuhiala, H.J. (2008b) Seeing direct and averted gaze activates the approach–avoidance motivational brain systems. *Neuropsychologia* 46, 2423–2430.
- Hietanen, J.K., Nummenmaa, L., Nyman, M.J., Parkkola, R. and Hämäläinen, H. (2006) Automatic attention orienting by social and symbolic cues activates different neural networks: an fMRI study. *NeuroImage* 33, 406–413.
- Hochstein, S. and Ahissar, M. (2002) View from the top: hierarchies and reverse hierarchies in the visual system. *Neuron* 36, 791–804.
- Hoffman, E.A. and Haxby, J.V. (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience* 3, 80–84.
- Jacob, P. (2008) What Do Mirror Neurons Contribute to Human Social Cognition? *Mind & Language* 23, 190–223.
- Jellema, T., Baker, C.I., Wicker, B. and Perrett, D.I. (2000) Neural representation for the perception of the intentionality of actions. *Brain and Cognition* 44, 280–302.
- Kampe, K.K.W., Frith, C.D. and Frith, U. (2003) “Hey John”: signals conveying communicative intention toward the self activate brain regions associated with “mentalizing,” regardless of modality. *The Journal of Neuroscience* 23, 5258–5263.
- Kendon, A. (1994) Do Gestures Communicate? A Review. *Research on Language & Social Interaction* 27, 175–200.
- Kingstone, A., Friesen, C.K. and Gazzaniga, M.S. (2000) Reflexive joint attention depends on lateralized cortical connections. *Psychological Science* 11, 159–166.
- Kingstone, A., Tipper, C., Ristic, J. and Ngan, E. (2004) The eyes have it!: an fMRI investigation. *Brain and Cognition* 55, 269–271.
- Klein, J.T., Shepherd, S.V. and Platt, M.L. (2009) Social attention and the brain. *Current Biology* 19, R958–962.
- Kleinke, C.L. (1986) Gaze and eye contact: a research review. *Psychological Bulletin* 100, 78–100.

- Koechlin, E. and Jubault, T. (2006) Broca's area and the hierarchical organization of human behavior. *Neuron* 50, 963–974.
- Kveraga, K., Ghuman, A.S. and Bar, M. (2007) Top-down predictions in the cognitive brain. *Brain and cognition* 65, 145–168.
- Lachat, F., Hugueville, L., Lemaréchal, J.-D., Conty, L. and George, N. (2012) Oscillatory Brain Correlates of Live Joint Attention: A Dual-EEG Study. *Frontiers in Human Neuroscience* 6, 156.
- Langton, S.R. and Bruce, V. (2000) You must see the point: automatic processing of cues to the direction of social attention. *Journal of Experimental Psychology. Human Perception and Performance* 26, 747–757.
- LeDoux, J.E. (2000) Emotion circuits in the brain. *Annual Review of Neuroscience* 23, 155–184.
- Materna, S., Dicke, P.W. and Thier, P. (2008) The posterior superior temporal sulcus is involved in social communication not specific for the eyes. *Neuropsychologia* 46, 2759–2765.
- McNeill, D. (1992) *Hand and Mind*. Univeristy of Chicago Press, Chicago.
- Meadows, J.C. (1974) The anatomical basis of prosopagnosia. *Journal of Neurology, Neurosurgery, and Psychiatry* 37, 489–501.
- Mehu, M., D'Errico, F. and Heylen, D. (2012) Conceptual analysis of social signals: the importance of clarifying terminology. *Journal on Multimodal User Interfaces* 6, 179–189.
- Müller, H.J. and Rabbitt, P.M. (1989) Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *Journal of Experimental Psychology. Human Perception and Performance* 15, 315–330.
- N'Diaye, K., Sander, D. and Vuilleumier, P. (2009) Self-relevance processing in the human amygdala: gaze direction, facial expression, and emotion intensity. *Emotion* 9, 798–806.
- Nagata, Y., Bayless, S.J., Mills, T. and Taylor, M.J. (2012) Spatio-temporal localisation of attentional orienting to gaze and peripheral cues. *Brain Research* 1439, 44–53.

- Nakamura, A., Maess, B., Knösche, T.R., Gunter, T.C., Bach, P. and Friederici, A.D. (2004) Cooperation of different neuronal systems during hand sign recognition. *NeuroImage* 23, 25–34.
- Nummenmaa, L., Passamonti, L., Rowe, J., Engell, A.D. and Calder, A.J. (2010) Connectivity analysis reveals a cortical network for eye gaze perception. *Cerebral cortex* 20, 1780–1787.
- Ousdal, O.T., Jensen, J., Server, A., Hariri, A.R., Nakstad, P.H. and Andreassen, O.A. (2008) The human amygdala is involved in general behavioral relevance detection: evidence from an event-related functional magnetic resonance imaging Go-NoGo task. *Neuroscience* 156, 450–455.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. and Rizzolatti, G. (1992) Understanding motor events: a neurophysiological study. *Experimental Brain Research* 91, 176–180.
- Pelphrey, K.A., Singerman, J.D., Allison, T. and McCarthy, G. (2003) Brain activation evoked by perception of gaze shifts: the influence of context. *Neuropsychologia* 41, 156–170.
- Pessoa, L. and Adolphs, R. (2010) Emotion processing and the amygdala: from a “low road” to “many roads” of evaluating biological significance. *Nature Reviews. Neuroscience* 11, 773–783.
- Posner, M.I. (1980) Orienting of attention. *The Quarterly Journal of Experimental Psychology* 32, 3–25.
- Puce, A. and Perrett, D. (2003) Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 358, 435–445.
- Raz, A. and Buhle, J. (2006) Typologies of attentional networks. *Nature Reviews. Neuroscience* 7, 367–379.
- Redcay, E., Kleiner, M. and Saxe, R. (2012) Look at this: the neural correlates of initiating and responding to bids for joint attention. *Frontiers in Human Neuroscience* 6, 169.
- Ristic, J., Friesen, C.K. and Kingstone, A. (2002) Are eyes special? It depends on how you look at it. *Psychonomic Bulletin & Review* 9, 507–513.

- Rizzolatti, G., Fadiga, L., Gallese, V. and Fogassi, L. (1996) Premotor cortex and the recognition of motor actions. *Brain Research. Cognitive Brain Research* 3, 131–141.
- Roy, M., Shohamy, D. and Wager, T.D. (2012) Ventromedial prefrontal-subcortical systems and the generation of affective meaning. *Trends in Cognitive Sciences* 16, 147–156.
- Saito D.N., Tanabe H.C., Izuma K., Hayashi M.J., Morito Y., Komeda H., Uchiyama H., Kosaka H., Okazawa H., Fujibayashi Y., Sadato N. (2010) “Stay tuned”: inter-individual neural synchronization during mutual gaze and joint attention. *Frontiers in Integrative Neuroscience* 4, 127.
- Sander, D., Grafman, J. and Zalla, T. (2003) The human amygdala: an evolved system for relevance detection. *Reviews in the Neurosciences* 14, 303–316.
- Sander, D., Grandjean, D., Kaiser, S., Wehrle, T. and Scherer, K.R. (2007) Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. *European Journal of Cognitive Psychology* 19, 470–480.
- Sapir, A., Soroker, N., Berger, A. and Henik, A. (1999) Inhibition of return in spatial attention: direct evidence for collicular generation. *Nature Neuroscience* 2, 1053–1054.
- Sato, W., Kochiyama, T., Uono, S. and Yoshikawa, S. (2009) Commonalities in the neural mechanisms underlying automatic attentional shifts by gaze, gestures, and symbols. *NeuroImage* 45, 984–992.
- Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T. and Vogeley, K. (in press) Toward a second-person neuroscience. *Behavioral and Brain Sciences*.
- Schilbach L., Wilms M., Eickhoff S.B., Romanzetti S., Tepest R., Bente G., Shah N.J., Fink G.R., Vogeley K. (2010) Minds made for sharing: initiating joint attention recruits reward-related neurocircuitry. *Journal of Cognitive Neuroscience* 22, 2702–2715.
- Schilbach, L., Wohlschlaeger, A.M., Kraemer, N.C., Newen, A., Shah, N.J., Fink, G.R. and Vogeley, K. (2006) Being with virtual others: Neural correlates of social interaction. *Neuropsychologia* 44, 718–730.

- Senju, A. and Johnson, M.H. (2009) The eye contact effect: mechanisms and development. *Trends in Cognitive Sciences* 13, 127–134.
- Shepherd, S.V. and Capuccio, M. (2011) Sociality, Attention, and the Mind's Eyes. In: *Joint Attention: New Developments in Psychology, Philosophy of Mind, and Social Neuroscience*. Axel Seemann. .
- Shepherd, S.V., Klein, J.T., Deaner, R.O. and Platt, M.L. (2009) Mirroring of attention by neurons in macaque parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America* 106, 9489–9494.
- Tettamanti M., Buccino G., Saccuman M.C., Gallese V., Danna M., Scifo P., Fazio F., Rizzolatti G., Cappa S.F., Perani D. (2005) Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience* 17, 273–281.
- Thompson, J.C., Hardee, J.E., Panayiotou, A., Crewther, D. and Puce, A. (2007) Common and distinct brain activation to viewing dynamic sequences of face and hand movements. *NeuroImage* 37, 966–973.
- Tipper, C.M., Handy, T.C., Giesbrecht, B. and Kingstone, A. (2008) Brain responses to biological relevance. *Journal of Cognitive Neuroscience* 20, 879–891.
- Tipples, J. (2002) Eye gaze is not unique: automatic orienting in response to uninformative arrows. *Psychonomic Bulletin & Review* 9, 314–318.
- Tomasello, M. (1995) Joint attention as social cognition. In: *Joint attention: Its origins and role in development*. Moore, Chris; Dunham, Philip J. Hillsdale, NJ, England: Lawrence Erlbaum Associates.
- Tomasello, M. (1999) *The Cultural Origins of Human Cognition*. Harvard University.
- Tomasello, M. and Carpenter, M. (2007) Shared intentionality. *Developmental Science* 10, 121–125.
- Tomasello, M., Carpenter, M., Call, J., Behne, T. and Moll, H. (2005) Understanding and sharing intentions: the origins of cultural cognition. *The Behavioral and Brain sciences* 28, 675–691; discussion 691–735.
- Tomasello, M., Carpenter, M. and Liszkowski, U. (2007) A new look at infant pointing. *Child Development* 78, 705–722.

- Ulloa, J.L., Puce, A., Hugueville, L. and George, N. (in press) Sustained neural activity to gaze and emotion perception in dynamic social scenes. *Social Cognitive and Affective Neuroscience*.
- Vecera, S.P. and Rizzo, M. (2004) What are you looking at? Impaired “social attention” following frontal-lobe damage. *Neuropsychologia* 42, 1657–1665.
- Waytz, A., Gray, K., Epley, N. and Wegner, D.M. (2010) Causes and consequences of mind perception. *Trends in Cognitive Sciences* 14, 383–388.
- Wheaton, K.J., Thompson, J.C., Syngienotis, A., Abbott, D.F. and Puce, A. (2004) Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *NeuroImage* 22, 277–288.
- Willems, R.M. and Hagoort, P. (2007) Neural evidence for the interplay between language, gesture, and action: a review. *Brain and Language* 101, 278–289.
- Williams, J.H.G., Waiter, G.D., Perra, O., Perrett, D.I. and Whiten, A. (2005) An fMRI study of joint attention experience. *NeuroImage* 25, 133–140.
- Xu, J., Gannon, P.J., Emmorey, K., Smith, J.F. and Braun, A.R. (2009) Symbolic gestures and spoken language are processed by a common neural system. *Proceedings of the National Academy of Sciences of the United States of America* 106, 20664–20669.