

Other Minds

*How Humans Bridge the Divide
between Self and Others*

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BERTRAM F. MALLE
SARA D. HODGES

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Is There a "Social Brain"?

*Lessons from Eye-Gaze Following,
Joint Attention, and Autism*

DIEGO FERNANDEZ-DUQUE
JODIE A. BAIRD

The aim of this volume is to explore what it means to understand other minds. Drawing on philosophical, developmental, and psychological perspectives, the chapters in this book address myriad issues, including how an understanding of minds develops, its significance for social interaction, and its relationship to other social and cognitive achievements. Our chapter brings yet another perspective to bear on these issues. Taking a neuroscientific approach, our discussion centers on how understanding other minds—a central aspect of social-information processing—is represented in the brain.

Currently in the literature there are two very different models of how the brain is organized for processing social information. One model posits the existence of a "social brain." In this view, the human mind has evolved a set of domain-specific solutions to particular social problems. According to this view, there exists a set of mental systems for perceiving and reasoning about social stimuli that act independently from the mental systems involved in perceiving and reasoning about nonsocial things. It is the content of the information—its social nature—that determines

the dichotomy, rather than the structure of the problem (Cosmides & Tooby, 1992). These social modules are thought to be unique in their input (i.e., the information they process) as well as in their mechanism (i.e., the rules that govern their processing). Finally, their content specificity is ostensibly caused by phylogenetic evolution rather than by familiarity, expertise, or ontogenetic development. In its neuroscientific aspect, the view posits the existence of dedicated brain areas for the processing of social information (Duchaine, Cosmides, & Tooby, 2001).

A different model, with origins in information-processing research, views the mind as a set of subsystems, each of which processes a collection of basic computations. Although the model allows for the existence of domain-specific processes and algorithms, this is not its defining feature. Rather, what dictates which brain areas become engaged are the computational operations necessary to solve the problem. Most cognitive neuroscience research in attention, memory, imagery, and executive functions has followed this information-processing approach (Posner & Raichle, 1994).

Tasks of social relevance often engage the same network of brain areas. At first glance, this appears consistent with the idea of a "social brain." However, those brain areas are sometimes driven by nonsocial tasks too, which contradicts the "social brain" argument. A main goal of this chapter is to put forward a synthesis that accommodates these disparate results. In agreement with information-processing models, we argue that there is no "social brain" but rather isolable subsystems that perform basic computations. But how does this account for the fact that social tasks tend to activate the same network of brain areas? We argue that the recruitment of similar areas by social stimuli happens because social stimuli disproportionately tap into certain basic computations, such as those related to affective processes. Importantly, this correlation between social stimuli and basic computations is not perfect, leaving room for nonsocial stimuli to engage those same brain areas, and also allowing social stimuli *not* to engage those areas on occasion. The absence of a perfect correlation between social stimuli and basic computational operations also makes the distinction between these two levels useful and theoretically important rather than a mere redescription of the same phenomena.

As evidence for our main thesis, we focus on one social skill in particular—namely, the ability to detect and follow eye gaze. We review behavioral and neurological findings on eye-gaze following and discuss its relation to other perceptual skills of social importance, such as facial emotion recognition and face identification. Next, we discuss whether eye-gaze following is related to mental state attributions and joint attention. We end with a discussion of how the impairment of these abilities in autism

may both shed light on their typical development and provide answers to how the brain is organized in its processing of social information.

EYE-GAZE PERCEPTION: BEHAVIORAL EVIDENCE

Both in humans and other primates, the ability to follow the direction of gaze is of great importance for social interaction. Primates such as chimpanzees and macaques spontaneously follow the eye gaze of conspecifics, and direction of gaze conveys social dominance (Tomassello, Call, & Hare, 1998). Humans automatically cue their attention in the direction of gaze: 3-month-old infants can follow perceived gaze (Hood, Willen, & Driver, 1998), and even newborns can discriminate between direct and averted gaze, thus suggesting a strong inborn determinism (Farroni, Csibra, Simion, & Johnson, 2002). What is less clear is whether and to what extent these processes are related to mental state attributions. In nonhuman primates, eye-gaze following appears to be a stimulus-driven, nonmentalistic process (Povinelli, Bering, & Giambrone, 2000). In human adults, mental state inferences may not be necessary, even if mental attributions often coexist with gaze following. This counterintuitive fact is well known to any basketball player who has found him- or herself following the adversary's gaze despite knowing the latter's intention to deceive. In experimental paradigms, subjects automatically follow the direction of the eyes even when eye gaze predicts that the target will occur in the opposite location (Driver et al., 1999). These findings, together with the early development of eye-gaze cueing in infancy, suggest a rigid, nonmentalistic system of gaze following that is driven by the physical properties of the stimulus, such as the relation of the dark iris to the white sclera (Ricciardelli, Baylis, & Driver, 2000) and possibly also by the orientation of the head (Langton, Watt, & Bruce, 2000).

EYE-GAZE PERCEPTION: NEUROLOGICAL EVIDENCE

The system for eye-gaze detection is ideal for exploring neural mechanisms of relevance to social interactions even if, in itself, eye-gaze detection is an elementary part of social behavior. For one, eye-gaze detection can be explored with invasive methods in nonhuman primates, yielding highly specific and localized information. Second, since eye-gaze perception is relatively independent from language, it is less problematic to make generalizations across species. Finally, since eye-gaze detection is driven by external stimuli, it is possible to systematically manipulate the system.

The first question to address is whether there is an isolable neural system for eye-gaze detection in its most rudimentary form. Over the last two decades, neuroscience has provided several good examples of that type of direct mapping. Here we briefly mention two such mappings before describing the eye-gaze system. The first example is a region of the posterior temporal lobe, area MT, which has been implicated as a direct neural correlate of perceived visual movement. Neurons in area MT respond selectively to the direction and velocity of movement, and their electrical stimulation biases the behavioral response to moving stimuli (Salzman, Murasugi, Britten, & Newsome, 1992). Area MT is activated by the aware perception of motion (Tootell et al., 1996). The second example is the fusiform face area (FFA), an area of the ventral temporal occipital cortex that responds selectively to faces. Lesion to the FFA leads to impaired recognition of facial identity (Damasio, Damasio, & Van Hoesen, 1982). Subjective experience of faces activates this area even in the absence of sensory stimuli, as in the case of visual imagery (O'Craven & Kanwisher, 2000).

Along the same lines, several studies have pointed to an area of the posterior part of the superior temporal sulcus (STS) as critical for the encoding of eye gaze. In neuroimaging studies, this area is activated by faces changing the direction of gaze and even by static displays of faces with averted eyes (Allison, Puce, & McCarthy, 2000; Wicker, Perret, Baron-Cohen, & Decety, 2003). Single-neuron recording studies in monkeys reveal some neurons in the anterior part of the STS that respond specifically to gaze direction (Perrett, Hietanen, Oram, & Benson, 1992), and gaze perception is disrupted by lesions to this area (Campbell, Heywood, Cowey, Regard, & Landis, 1990).

EYE-GAZE PROCESSING: SOCIAL MODULE OR INFORMATION PROCESSING?

The literature reviewed thus far illustrates the critical role of the STS in eye-gaze perception. Given the importance of eye-gaze perception in primate social behavior, some may argue that the STS constitutes evidence for the modularity of the social brain. The strongest version of such a modularity claim would argue that the computation of eye-gaze direction is "encapsulated" in the STS. According to this view, other stimulus properties such as facial emotion, and the context in which they are displayed, should have no influence on the system. A less stringent version of the "social brain" hypothesis allows for modulation by other social input (e.g., facial emotion), although not by general resources (e.g., at-

tion). Neither version allows for the processing of social and non-social stimuli by common brain areas.

In what follows, we present evidence against both versions of the "social modularity in the brain" hypothesis. Against the strong version of modularity, behavioral and neurophysiological data reveal rich interactions between eye gaze and other facial processes. Against the weaker version of the "social brain" hypothesis, data reveal modulation by general resources and anatomical commonality in the neural instantiation of social and nonsocial processes.

THE RELATION OF EYE-GAZE PERCEPTION TO OTHER ASPECTS OF FACIAL INFORMATION PROCESSING: BEHAVIORAL AND ELECTROPHYSIOLOGICAL EVIDENCE

Even though eye-gaze perception depends critically on the STS, the impact of eye gaze on behavior is modulated by other factors. For example, faces expressing emotion modulate gaze-evoked shifts of attention. Thus, when the person whose eyes serve as a cue looks happy, attention is sustained, but when the person looks angry, attention is relocated somewhere else (Fenske, Frisken, & Tipper, 2004). Furthermore, fearful faces are more effective at cueing attention than neutral faces, at least in subjects who are anxiety-prone (Mathews, Fox, Yiend, & Calder, 2003). Eye gaze also interacts with facial recognition in that faces with direct gaze are easier to identify than faces with averted gaze (Macrae, Hood, Milne, Rowe, & Mason, 2002).

These interactions among gaze, facial emotion, and facial identity also extend to their neural substrates. The activation of the amygdala, a region involved in emotion recognition, is modulated by the direction of gaze. When faces with neutral expression are displayed, direct gaze leads to stronger activation of the fusiform face area than averted gaze and also increases the functional connectivity between amygdala and the fusiform face area (George, Driver, & Dolan, 2001). A likely interpretation is that the emotional valence conveyed by a direct gaze gets encoded in the amygdala, which in turn modulates the fusiform face area via its feedback projections to improve facial identity recognition. The amygdala also appears to be an integral part of the system for eye-gaze detection, as it is activated by eye gaze and its lesion impairs gaze perception (Kawashima et al., 1999; Young et al., 1995).

The amygdala and STS have bilateral anatomical projections, and both areas send projections directly to the orbitofrontal cortex (OFC), an area critical for emotion regulation (Rolls, 1999). Finally, the STS has

functional connectivity with regions important for shifting visuospatial attention to the periphery, such as the intraparietal sulcus, thus being an integral part of the neural circuit for eye-gaze following (George et al., 2001).

The behavioral, functional, and anatomical results described above reveal a network of brain structures, including area MT, FFA, STS, amygdala, and OFC, which act in concert to compute many aspects of facial information that are important for social interactions. Much like the findings from other cognitive systems, these results reveal a division of labor, with each area performing a computation that is smaller than the task as a whole. At the same time, each subsystem is heavily modulated by general resources such as the allocation of attention, thus arguing against any type of strong modularity. For example, when the task requires that subjects pay attention to eye gaze, the activity of the STS is increased, while the activation of the FFA, the area that encodes the structural aspect of faces, remains invariant. As expected, paying attention to face identity leads to the opposite pattern (Hoffman & Haxby, 2000).

SOCIAL AND NONSOCIAL PROCESSES: ANATOMICAL COMMONALITY

The literature reviewed thus far argues that the processing of facial information is instantiated by a network of brain structures that includes, among others, area MT, FFA, STS, amygdala, and OFC. These areas are heavily interdependent and modulated by general resources such as attention.

The available evidence also argues against a brain area—or even a network of areas—dedicated to the exclusive processing of social stimuli. For example, area MT responds to biological motion, but it also responds to random dot movement (Salzman et al., 1992). The STS is sensitive to eye gaze, but it is also sensitive to aspects of language (Martin, 2003), semantic knowledge (Chao, Haxby, & Martin, 1999), visuospatial attention, and target detection (Corbetta & Shulman, 2002). The amygdala is important for eye-gaze detection and the recognition of facial expressions of fear, but it also processes many other aspects of fear—for example, Pavlovian classical conditioning and response to aversive tastes and odors (Davis & Whalen, 2001). The orbitofrontal cortex may be important for recognizing certain facial emotions, but it is also critical for modulating nonsocial stimulus-reward associations, such as the relation between key press and food (Blair, 2003; O'Doherty et al., 2003). The role of the OFC appears to be a more general modula-

tion of stimulus-reward associations, of which facial emotions and direct gaze may be special cases. These are just a few examples of how a brain area can be recruited by social stimuli even if the area also participates in other, nonsocial processes. Finally, although parts of the fusiform gyrus are particularly sensitive to faces, which are a type of social stimuli, these same brain areas are also sensitive to nonsocial stimuli that are globally encoded, such as expert recognition of cars or birds (Gauthier & Nelson, 2001).

In sum, there is a network of brain regions disproportionately engaged by social stimuli such as faces. But those areas are also engaged in basic computations of no social relevance. Thus, their engagement by social stimuli is insufficient proof for the existence of a "social brain." Rather, it suggests that social stimuli often carry particular properties—valence, reward value, spatial arrangement of its features—that disproportionately tap certain basic operations.

EYE-GAZE PERCEPTION: A WINDOW INTO MENTAL STATE ATTRIBUTION?

There is no doubt that encoding and following eye gaze are important social skills for both human and nonhuman primates. Nor is there any doubt that normal human adults often make mental state attributions about the eye-gaze patterns they detect: when an agent directs his or her eyes to an object, adults infer that he or she is *seeing* the object (i.e., creating a mental representation that can be used for guiding future behavior, enriching knowledge, and so forth). For normal human adults, the behavioral description (eye gaze) and its mentalistic redescription (seeing) almost always go hand in hand. Moreover, during development, the covariance between the mentalistic and nonmentalistic levels (i.e., between the "looking at" and the alignment of gaze direction and attended object) may play a role in fostering the emergence of mental state attribution. That is, such covariance may help to bootstrap mental state attribution in typically developing human infants who are experience-ready. But there is no principled reason why this should be true in other populations. Newborns, monkeys, and individuals with autism may detect and follow eye gaze without taking the extra step of attributing mental states to such behaviors (Povinelli et al., 2000).

On the whole, knowing about eye-gaze detection tells us little about whether mental state attributions are being made. Similarly, identifying the brain areas involved in eye-gaze detection tells us little about which areas are critical, or even necessary, for the attribution of mental states. Just because behavior and mental states tend to co-occur does not mean

that the same brain areas involved in detecting the behavior would also be involved in the attribution of mental states to that behavior. To put it bluntly, computing the direction of gaze is not the same as using the direction of gaze to infer another's intention, nor need it depend on the same brain structures.

DEVELOPMENT: FROM REFLEXIVE EYE CUEING TO JOINT ATTENTION

So far, we have been describing the rudimentary system of eye-gaze detection, but in typically developing humans this rudimentary system becomes part of a more sophisticated system rather quickly in development. At the age of 9 months, infants start using direction of gaze in a flexible manner that takes into account people's communicative intentions, a skill that forms part of what has been labeled "joint attention." Joint attention is the ability to coordinate attention between interactive social partners with respect to objects or events. It reveals an understanding by infants that adults are intentional agents, that is, that adults voluntarily attend to objects and that their attention can be shared, directed, and followed. Besides responding to another's gaze shift, joint attention includes behaviors such as proto-declarative pointing (i.e., pointing to refer to an object, as opposed to pointing to request an object), imitative learning (i.e., acting on objects in the way that adults are acting on them), and social referencing (i.e., infants' reference to adults for information about the approachability, desirability, and other features of objects) (Tomasello & Rakoczy, 2003). All four of these skills—the flexible use of eye-gaze following, proto-declarative pointing, imitative learning, and social referencing—are correlated, develop in synchrony between the ages of 9 and 24 months, and show little influence from environmental variables. Across these behaviors, there seems to be the expression of a single underlying skill—the understanding of persons as intentional agents—which is almost completely absent in other primates (Povinelli et al., 2000; Tomasello & Rakoczy, 2003). As such, it may be the single most important developmental milestone in the understanding of other minds. At the same time, the features that make it so remarkable, namely its early emergence in development and its exclusivity to humans, are the same that make it inaccessible to most of the methods of cognitive neuroscience. Although adult neuropsychology and neuroimaging provide good approximations and hypotheses, it would be erroneous to simply extrapolate from these models to the case of development (Karmiloff-Smith, 1998). Therefore, researchers have been interested in

diseases of development, autism in particular, to provide a more complete picture of how these developing abilities map onto brain structures.

DEVELOPMENTAL DISORDERS: THE CASE OF AUTISM

Autism is a neurodevelopmental disorder with a strong genetic component and a heterogeneous neurological substrate. Abnormalities have been reported in the limbic system (anterior cingulate, amygdala, hippocampus, and orbitofrontal cortex), cerebellum, frontal lobes, superior temporal gyrus, and subcortical structures including the thalamus and the basal ganglia (Lord, Cook, Leventhal, & Amaral, 2000). This broad range of neurological abnormalities is matched at the behavioral level by a broad phenotype that includes motor, linguistic, social, and emotional deficits (Joseph, 1999). Individuals with autism exhibit stereotypic and repetitive motor behavior, and their use of language is both delayed and disrupted. At its core, however, autism is a disorder of social interaction and communication.

Poor eye-gaze following is a specific marker of autism, and one of its earliest signs, evident in children as young as 18 months of age. Some children with autism even fail to use gaze as a cue to locate an object (Leekam & Moore, 2001). This is especially remarkable given that chimpanzees, who are incapable of joint attention, can nevertheless use gaze as an instrumental cue (Povinelli et al., 2000). In one study, school-age children with autism were tested in a naturalistic environment for their ability to use eye gaze as an orienting cue. In the autistic group, children with high mental age performed normally, but those with low mental age were impaired relative to developmentally delayed children matched for mental age. Autistic children of low mental age were capable of following gaze when a target object was observable (a skill that emerges at 6 months of age in typically developing infants) but were impaired when the target was absent (a skill that normally develops at the age of 9 months and that indicates the emergence of joint attention; Leekam & Moore, 2001). Another study tested high-functioning 10-year-olds with autism in a computer-based paradigm and found normal cueing effects (Sweetenham, Condie, Campbell, Milne, & Coleman, 2003). Taken together, these two studies suggest that eye-gaze cueing deficits in autism vary according to the severity of impairment in general intelligence.

In contrast, joint attention deficits in autism occur independently of general intelligence and are an early marker of the disease. Children with

autism show deviant patterns of reciprocal gaze behavior with their caregivers as well as deficits in the triadic coordination among themselves, adult, and object (Charman, 2003). Interestingly, joint attention in 3- and 4-year-old children with autism is positively correlated with orbitofrontal function, as measured by tasks that engage this region in normal subjects (Dawson et al., 2002). Orbitofrontal cortex is necessary for adding flexibility to stimulus-reward associations (Fellows & Farah, 2003; Rolls, 1999). An inability to assign stimulus-reward associations and flexibly modify them could be detrimental to the development of joint attention, as joint attention depends on social rewards, such as smiles, that are more variable than nonsocial rewards. Consistent with this hypothesis, autistic infants and toddlers prefer highly contingent, nonvariable feedback, while typically developing children instead prefer variable, imperfect feedback (Gergely & Watson, 1999). The contingency hypothesis illustrates the main problem of arguing for a module devoted exclusively to social stimuli. Even if certain brain regions do process social stimuli preferentially, it does not follow that such preferential processing is due to the "social" nature of the stimuli. In the aforementioned example, the driving force is the variability of the stimulus-reward association, which is typical of social stimuli but can be present in nonsocial stimuli as well.

Individuals with autism also show abnormalities in the processing of facial and emotional stimuli. Studies measuring event-related potentials (ERPs) reveal that children with autism are impaired in the discrimination of novel versus familiar faces, despite their normal discrimination of novel versus familiar objects. Relative to healthy adults, adults with autism have reduced response to facial emotions. This includes abnormal activity in the fusiform gyrus, amygdala, and the STS (Crichtley et al., 2000). One possible interpretation of these data is that they provide evidence for a social perception module whose impairment in autism accounts for the social deficits exhibited by this group. Although this analysis captures much of what is wrong in autism, it makes the same mistake previously described in our analysis of stimulus-reward associations. Just because social stimuli such as faces happen to activate the fusiform face area, it does not follow that faces activate this area *because* they are stimuli of social relevance. Nonsocial stimuli such as cars and birds can similarly activate this region, provided that observers are experts in recognizing those objects and encode them globally. The critical factor, therefore, seems to be not the social nature of the stimulus but its holistic encoding. Of course, this is not to say that difficulties in face perception, emotion recognition, and gaze following do not have consequences for mental state inferences. On the contrary, such deficits may put children with autism at a severe disadvantage in their development

of mental state understanding. Relative to typically developing children, children with autism have difficulties using the eyes as cues for attributing mental states (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001) and in using faces to judge the approachability and trustworthiness of people (Adolphs, Sears, & Piven, 2001). There is also evidence that children with autism have difficulty understanding gaze in mentalistic terms (Baron-Cohen, 1995).

So, is autism best characterized as a deficit in a social module or as a disorder of basic processes that apply to both social and nonsocial domains? Individuals with autism have deficits in joint attention and mental state attributions, but they also have motor deficits, visual attention deficits, and deficits in feedback processing, set switching, executive processing, and other nonsocial abilities (Joseph, 1999). Thus, although autism may present first and foremost as a problem of social cognition, it also manifests itself in nonsocial problems. This dual deficit poses a challenge to both the social module view (why should there be nonsocial deficits?) and the information-processing view (why should the deficit be mostly social?). Our proposal is that the solution to this paradox lies not in the brain itself but in the external stimuli that the brain processes. More specifically, we argue that attributes of social stimuli may correlate with basic information-processing computations. According to our framework, a deficit in the basic computation would affect primarily, but not exclusively, the processing of social information. We have already discussed the examples of variable stimulus-reward associations and holistic visual encoding. In both cases, there is a correlation between the type of stimulus (social/nonsocial) and a computational feature (variable/nonvariable reward; holistic/feature-based encoding). We are not claiming that these two basic computations account for all deficits in autism; rather, we use these examples to illustrate the larger point that general computational deficits may account for what appear to be domain-specific deficits.

Stimulus category (social/nonsocial) may correlate with other basic computations, such as those involved in affective processing. Since social stimuli carry more affective valence than nonsocial stimuli, they should disproportionately tap limbic structures such as the amygdala and the orbitofrontal cortex. Limbic areas are activated by affective stimuli such as faces. These brain areas send feedback projections to regions of the temporal lobe including the fusiform gyrus. During normal development, this affective loop is likely to play a role in modulating the plasticity of the fusiform gyrus, which with experience becomes a dedicated system for face recognition (i.e., the FFA). To put it in psychological terms, faces are attractive stimuli that capture the child's attention, thus becoming the focus of preferred processing and, with the passage of

time, a stimulus the child is expert with. But for children with autism, faces do not seem to carry their appropriate valence, and thus these children seem uninterested in faces. Within a social module framework, there is little one could do to rectify this problem. Within an information-processing framework, however, it should be possible to pair facial stimuli with nonsocial rewards that are valued by the autistic child and in this way engage the affective loop. Through extensive training in such a paradigm, it might be possible for children with autism to achieve the type of expertise with facial stimuli that typically developing children gain naturally (Carver & Dawson, 2002).

Also related to the affective dimension, type of stimulus (social/nonsocial) may correlate with orienting effectiveness. For example, while the orienting deficit in autism is most severe for social stimuli, such as faces or being called by name, individuals with autism are also impaired in their orienting to nonsocial stimuli, such as a jack-in-the-box (Dawson, Meltzoff, Osterling, Rinaldi, & Brown, 1998). Interestingly, deficits in joint attention correlate with deficits in orienting toward social stimuli but not with nonsocial orienting. This result is consistent with the idea raised earlier that the covariance of mental and nonmental levels (orienting to a location, finding a social stimulus at that location) may foster the mental state attribution process.

CONCLUSIONS

The mind's redescription of social information into basic information-processing computations may prove to be a powerful tool. We mentioned examples in the context of autism, but it is easy to see how the logic can generalize to typical development. Importantly, such redescription provides the system for processing social stimuli with a flexibility that is central to social interactions and that a social module framework cannot easily account for. Imagine that somebody stares at you with an angry face. Depending on the context, you might feel amused (the person is an actor you are watching in a play), frightened (you are in a shady part of town), or disgusted (the person is the leader of the world superpower justifying his next imperialistic move). In other words, it is easy to imagine that one and the same stimulus will be processed very differently depending on the context (Lange et al., 2003). Such context effects cannot be explained by models positing a strict separation between social and nonsocial information. In contrast, an information-processing account can easily accommodate these contextual effects, as it assumes that general cognitive abilities can influence the processing of information. Reconceptualizing the social brain in terms of basic information processes also allows researchers to ask

how—in computational terms—social information is processed. Finally, it entrenches social neuroscience within the cognitive neuroscience tradition that has been so fruitful over the past two decades. Just as the brain does not make a strict separation between social and cognitive information, neither should brain researchers.

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