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Social Cueing Elicits a Distinct Form of Visual Spatial Orienting

EVIDENCE FROM BEHAVIORAL, NEUROIMAGING,
AND DEVELOPMENTAL RESEARCH

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Introduction

Orienting attention in the direction of another person's gaze, head turn, or finger point may represent a unique behavior that is distinct from traditionally identified types of orienting (i.e., exogenous and endogenous). In this chapter we explore the question of whether the attention orienting response to social cues is unique by reviewing cognitive-behavioral findings. We propose that current taxonomies do not adequately capture the construct of social orienting, and we present an adapted framework that is more elaborate in classifying both the degree to which orienting is consciously controlled and the extent to which learning and experience play a role in the acquisition of the social orienting response. We then review neuro-imaging and developmental findings (including specific examples of atypical development; autism and schizophrenia) in order to determine whether our proposed framework is supported by findings from these research disciplines.

Social Orienting of Attention

The sheer quantity of visual information that is available at any one moment necessitates that attention be selective based on salience or set priorities (Enns & Trick, 2006). The orienting system is responsible for shifting and redirecting attentional resources to process salient events in the environment. Orienting involves moving the focus of attention to a new location in the visual field. Often, salient visual events are given attentional priority by the orienting system on the basis of their relevance to the individual. Some visual events, such as flashes of light or sudden

movement in the visual periphery (e.g., exogenous cues), are oriented to in a reflexive manner by all healthy humans. Other visual stimuli, such as an arrow (e.g., endogenous cue) that points to the left, will cause attention to shift to the left only in individuals who have learned the meaning of the arrow symbol. A third category of visual stimuli, such as averted eye-gaze, head turns, body posture, and finger pointing, appears to trigger orienting of attention primarily because they facilitate social communication and thus are *socially* salient to most humans and to some extent other social animals (Driver et al., 1999; Friesen & Kingstone, 1998, 2003a, 2003b; Friesen, Moore, & Kingstone, 2005; Friesen, Ristic, & Kingstone, 2004; Langton, 2000; Langton & Bruce, 1999, 2000; Langton, Watt, & Bruce, 2000).

Social cues are likely prioritized by the human attention system because following the head turns, pointing, and eye-gaze of another person plays a fundamental role in the development of language and adaptive social functioning. Attending to directional social cues emerges in early infancy. At 3 months of age babies are able to shift their attention in response to an adult's averted gaze (Hood, Willen, & Driver, 1998), demonstrating an adult-like orienting response (i.e., reflexive) by 14 months of age (Farroni, Johnson, Brockbank, & Simion, 2000). Early emergence of this skill highlights its importance in human development. For example, gaze following is critical to developing an awareness of others' perspectives and intentions (Carpendale & Lewis, 2006; Emery, 2000) and facilitates word learning by allowing children to match a verbal utterance with a gazed-at object (Baldwin, 1995). Individual differences in gaze following in infancy are consistently found to predict language development later in life (Morales, Mundy, Delgado, Yale, Messinger, Neal, & Schwartz, 2000; Morales, Mundy, Delgado, Yale, Neal, & Schwartz, 2000; Morales, Mundy, & Rojas, 1998). Sensitivity to the social meaning of gaze-direction continues to develop into adulthood (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Baron-Cohen, Wheelwright, & Jolliffe, 1997) and is a predictor of adult social competence (Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Mundy & Sigman, 2006).

Because so much of social communication involves tracking, interpreting, and understanding the meaning of social cues, humans may have developed a specialized network of processes dedicated to orienting toward the location of other persons' attention. Orienting responses to social cues have been extensively studied in laboratory settings. The spatial cueing paradigm (Posner, 1980) is the most common technique for examining orienting to a variety of directional social cues such as head direction (Langton, 2000), finger pointing (Langton & Bruce, 2000), body posture (Langton et al., 2000), and even a tongue that protrudes to the left or right (Downing, Dodds, & Bray, 2004). Averted eye-gaze, however, has received the majority of research attention, perhaps because of the unique significance of eyes to social functioning. We therefore focus primarily on gaze cues while exploring the question of whether social cueing responses represent a unique form of attention shifting. With the exception of infancy studies, covert orienting (shifting of the attentional focal point without eye movement), as opposed to overt orienting

(shifting of attention associated with detectable body movements), is the focus of this review.

Behavioral Findings: Gaze Cueing of Attention

Spatial cueing paradigms are based on the principle that humans are faster to detect targets in attended locations versus unattended locations. In a typical spatial cueing task (see Fig. 9.1 for an example of a cueing task), participants are told to press a key when they have detected a target (e.g., a star or asterisk) on a computer screen. A typical task begins with the appearance of a fixation cross in the middle of the screen, which serves to redirect eye-gaze on each trial. The participants are then instructed to fix their attention upon a central point and to respond when they see the target. The target is preceded by a cue that is either valid (correctly indicates the target location), invalid (incorrectly indicates the target location), or neutral (gives no indication of target location). Valid cues may be labeled as “congruent” and invalid cues as “incongruent,” or valid trials may be called “cued” whereas invalid trials are referred to as “uncued.” Shorter reaction times (RTs) to targets in validly cued locations versus invalidly cued locations (also known as the cue-validity effect or facilitation) indicate that participants have oriented their attention to the cued location. The time interval between the cue and the target can be varied in order to obtain a temporal profile of the attentional effect (Posner, 1980). This time interval is referred to as the cue-to-target delay or stimulus onset asynchrony (SOA).

Within a spatial cueing task, cue type along with other factors such as cue-target predictability can be varied to elicit different forms of orienting. Cue types generally fall into one of two traditional categories, exogenous or endogenous; exogenous cues are typically spatial/peripheral (e.g., a flash of light in the location where the target will appear) and endogenous cues are directional/central (e.g., an arrow pointing toward the location where the target will appear). Exogenous cues are associated with stimulus-driven, bottom-up, or reflexive orienting, whereas endogenous cues are associated with top-down, goal-driven, or voluntary orienting (Jonides, 1981). Reflexive orienting occurs rapidly, is not sustained, and does not require conscious processing (Jonides, 1981). Specifically, reflexive orienting is quick (participants are faster to detect targets 100 ms after a congruent cue), short-lived (differences between congruent and incongruent RTs disappear by 700 to 800 ms if a cue is non-predictive), and obligatory (at short cue-target intervals, participants cannot stop shifting their attention in the direction of a brief flash of light even when that brief flash of light appears in a location that does not facilitate target detection 80% of the time). Reflexive or automatic orienting of attention is associated with short SOAs. Thus, reflexive orienting refers to stimulus-driven, automatic orienting that is typically captured by paradigms that incorporate sudden-onset peripheral luminance cues with short SOAs (100 ms to approximately 300 ms) (Muller & Rabbitt, 1989) and in non-predictive cue-target contingencies.

Voluntary refers to volitional or goal-directed shifting of attention in response to centrally presented informational cues (endogenous cues) that predict target location with high probability. Volitional orienting is effortful and engaged later and, therefore, is typically measured at longer (>300 ms) SOAs. Unlike reflexive orienting, voluntary orienting is slow to develop (i.e., deliberate orienting does not develop fully until age 7 to 9; Brodeur & Enns, 1997) and is susceptible to deterioration with age (Enns & Trick, 2006; Iarocci, Enns, Randolph, & Burack, 2009). Thus, voluntary orienting is typically captured by paradigms that incorporate centrally presented informational cues with long SOAs (300 ms +) and in predictive cue-target contingencies.

Spatial cueing paradigms have been adapted to assess orienting to gaze cues. In a typical gaze-cueing experiment, a trial will begin with the appearance of a face with blank or closed eyes instead of a fixation cross. The pupils then appear looking to the right or left after one of several possible SOAs (to track the time course of reflexive and volitional orienting). On valid trials, pupils accurately indicate the location of the target (i.e., pupils “look” right and target appears on the right). On invalid trials, targets appear in the location opposite that indicated by the pupils (i.e., pupil “looked” left and the target appeared on the right). Figure 9.1 shows a gaze-cueing paradigm. A gaze-cueing task may comprise non-predictive, predictive, and/or counter-predictive conditions, which serve to measure the level of volitional control that participants have over their orienting response. In a non-predictive condition cues do not reliably predict target location (e.g., 50% of gaze-cues are valid and 50% are invalid). In predictive conditions, gaze cues accurately predict target location on approximately 75% to 80% of trials, and in the counter-predictive conditions, 75% to 80% of trials are invalid. A cue-validity effect in a non-predictive condition indicates that orienting occurs reflexively, since attending to cues in a volitional manner would not improve target detection performance. The counter-predictive condition provides a more stringent test of the automaticity of

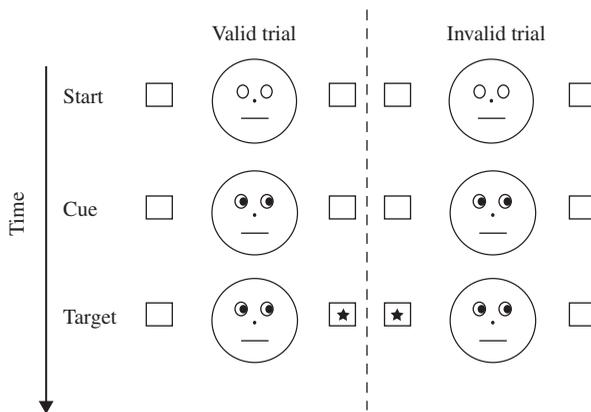


FIGURE 9.1. Example of a gaze-cueing paradigm with schematic stimuli.

orienting because, in theory, participants should shift their attention in the opposite direction than is indicated by invalid trials to improve their overall target detection performance. Thus, a cue-validity effect (i.e., faster target detection on valid trials) would indicate that despite conscious efforts to ignore cues, attention was oriented automatically in a counter-predictive condition.

At the behavioral level, orienting responses to eye-gaze appear to blur the distinction between traditional exogenous and endogenous orienting categories. Gaze cues are similar to endogenous/voluntary cues because they are informational and are typically centrally presented. However, gaze cues produce exogenous-like cueing effects and elicit faster RTs for valid versus invalid trials at shorter SOAs (100 to 300 ms) even when they are not spatially predictive (e.g., Driver et al., 1999; Friesen & Kingstone, 1998, 2003a, 2003b; Friesen et al., 2004, 2005; Langton, 2000; Langton & Bruce, 1999, 2000; Langton et al., 2000). Gaze elicits rapid (as fast as 14 ms after cue onset; Hietanen & Leppänen, 2003) and automatic shifting of spatial attention even when cues are counter-predictive (e.g., Friesen et al., 2004).

At first glance, gaze cues appear to elicit reflexive orienting although they are centrally presented. However, subtle differences in responses to gaze cues versus peripheral-onset cues exist. For instance, if gaze cues are reflexive in the traditional sense, then we expect to observe inhibition of return (IOR) effects. IOR is a key characteristic of reflexive orienting and refers to the suppression of orienting in the direction that has recently been the focus of attention for approximately 300 to 3,000 ms following initial cueing (Posner & Cohen, 1984). In early studies of IOR and gaze cueing, Friesen and Kingstone (2003a, 2003b) made the case that IOR and orienting to gaze were independent effects subserved by separate neural systems, yet subsequent reports revealed that IOR was triggered by gaze cues. For example, Frischen and Tipper (2004) observed IOR when they presented stimuli so that there was no temporal overlap between the gaze cue and target and attention was drawn away from the gazed-at location. Specifically, these authors observed prolonged facilitation triggered by gaze cues and inhibition at long (2,400 ms) SOAs. Similarly, Frischen, Smilek, Eastwood, and Tipper (2007) reported IOR at long SOAs when attention was drawn from the originally cued location. The authors concluded that whereas both gaze cues and sudden-onset cues elicit behaviorally similar orienting effects, there are subtle distinctions between the cue types. In contrast with sudden-onset cues, gaze cues elicit prolonged facilitation and a delayed IOR. Taken together, the results from IOR studies suggest that the behavioral orienting response to eye-gaze is similar yet subtly different from the classic reflexive response to peripheral-onset cues. Although the IOR results and the gaze-cueing effects at short SOAs in counter-predictive experimental conditions suggest that orienting responses to gaze cueing are unique, there are contradictory reports that gaze and arrows cues elicit behaviorally indistinguishable cueing effects.

Arrows trigger automatic orienting of attention when not spatially predictive (e.g., Hommel, Pratt, Colzato, & Godijn, 2001; Ristic, Friesen, & Kingstone, 2002; Tipples, 2002, 2008), contradicting the notion that only endogenous cues elicit

voluntary orienting (Jonides, 1981). For example, Hommel et al. (2001) observed reflexive orienting for both non-predictive arrow cues with orienting to non-predictive direction words (e.g., “up,” “down,” “left,” “right”) and concluded that over-learned communicative symbols can elicit reflexive effects. Similarly, Tipples (2002, 2008) also observed reflexive orienting to non-predictive arrow cues and concluded that eye-gaze is not unique with respect to triggering automatic orienting. Ristic et al. (2002) directly compared orienting responses to gaze and arrow cues in adults and preschoolers and found that at 195-ms, 600-ms, and 1,005-ms SOAs, both cues elicited responses that were behaviorally indistinguishable. These findings caused a shift in the way that researchers conceptualize “endogenous” cues but also threw into question the notion that eye-gaze is a special attentional cue because of its biological significance (e.g., Friesen & Kingstone, 1998; Langton & Bruce, 1999). In short, if the behavioral response to eyes is identical to that of a non-biologically significant arrow, then orienting in the direction of averted eye-gaze may not be a unique form of orienting.

An alternative possibility is that the differences between orienting to eyes and arrows are subtle and are not detected by employing the basic cueing paradigm. Findings suggest that in basic spatial cueing tasks, arrows and eyes may appear to elicit analogous orienting responses, but when tests are more stringent, subtle differences may become apparent. Several research groups have modified the cueing paradigm to compare orienting to arrows and eyes under more rigorous conditions in an effort to tease apart subtle differences. Friesen et al. (2004) compared orienting to arrows and gaze using counter-predictive cues. Participants were unable to resist shifting their attention first to the area indicated by averted gaze and then redirecting their attention toward the opposite direction where the target was most likely to appear. However, when shown a counter-predictive arrow cue, participants shifted their attention only toward the most likely target location (i.e., opposite to where the arrow pointed). Friesen et al. concluded that gaze cueing is “more reflexive” than arrow cueing. Similarly, Langdon and Smith (2005) observed that gaze cues elicited stronger orienting effects than arrows and that gaze cues triggered facilitation without costs at short SOAs. The authors concluded that gaze is a unique symbolic cue because it elicits a distinct orienting response, likely due to the biological relevance of eyes. An experiment by Ristic and Kingstone (2005) also suggested that when eyes are perceived, they elicit a “special pull” on attention. They presented participants with an ambiguous stimulus that could be perceived as a face with eyes or a car, and participants demonstrated involuntary shifting of attention only when they were told that the stimuli depicted eyes. Finally, Ristic, Wright, and Kingstone (2007) compared arrows and eyes in an experiment that utilized color contingencies (e.g., a blue arrow only facilitates orienting to blue targets). These authors replicated a previous finding (Pratt & Hommel, 2003) that reflexive orienting is elicited by arrows only when targets are color congruent. However, orienting to gaze occurred with color-congruent and color-incongruent targets. Whereas cue–target color contingency produced significant effects on performance for both

arrows and eyes, reflexive orienting to gaze cues was not affected by arbitrary cue–target color contingencies to the extent that arrows were. Therefore, the researchers concluded that the attention effect triggered by eye direction is “more strongly reflexive” than that triggered by arrows.

In sum, gaze cues consistently elicit distinct orienting responses that resemble, but are not identical to, orienting responses elicited by exogenous cues and endogenous cues such as arrows (but see Birmingham & Kingstone, 2009). Similar to peripheral flash cues, gaze cues elicit rapid orienting at short SOAs when cues are not predictive or counter-predictive (e.g., Friesen et al., 2004). Gaze cues also elicit IOR effects, but unlike peripheral flash cues, IOR effects are delayed and are associated with prolonged facilitation (Frischen, Smilek, et al., 2007). Like a traditional endogenous cue (e.g., an arrow), gaze cues elicit what appears to be reflexive orienting. However, gaze cues are likely “more reflexive” than arrow cues because they are not as susceptible to top-down control (Friesen et al. 2004; Langdon & Smith, 2005; Ristic, Wright, & Kingstone, 2007). It is possible that there is a range of reflexivity when it comes to orienting responses that is based on the relevance of the stimuli to the individuals. Ristic et al. (2007) suggest that “there is a range of central spatially non-predictive stimuli that engage spatial attention reflexively, with the strength of this reflexive orienting effect varying across stimuli” (p. 968). However, gradations of reflexivity are not consistent with the traditional dichotomous categorical orienting taxonomy, rendering gaze cueing difficult to classify.

Adapting a Taxonomy for Social Orienting

Orienting or cueing responses may be amenable to classification on continuous rather than categorical dimensions (see Frischen, Bayliss, & Tipper, 2007 for more details), a notion supported by behavioral evidence from gaze-cueing studies as well as findings that orienting to even abrupt-onset cues is under a certain amount of voluntary control (Folk & Remington, 1998). However, the findings from orienting studies are frequently interpreted within the confines of existing conceptual frameworks and limited to dichotomous terms such as bottom-up or top-down, exogenous or endogenous, automatic or deliberate, reflexive or voluntary. A few researchers (Frischen, Bayliss, & Tipper, 2007; Gibson & Kingstone, 2006) have argued for the reconsideration of traditional conceptual frameworks to ones that would allow for more nuanced approaches that take into account how and under what conditions orienting to gaze may be unique.

An adapted conceptual framework can be built upon existing frameworks such as that proposed by Enns and Trick (2006) for studying selective attention and serve as a template for creating an adapted orienting taxonomy. Within their framework, responses can be classified into two major dimensions: awareness and origin. The dimension of awareness addresses the degree to which orienting occurs with conscious control and ranges from automatic to controlled. According to Enns and

Trick, automatic selective attention is effortless, rapid, and triggered by the presence of certain stimuli in the environment. In contrast, controlled selective attention is conscious or intentional. The second dimension of Enns and Trick's framework, origin, refers to the extent to which learning plays a role in orienting. The dimension comprises two categories: exogenous and endogenous. Exogenous orienting is innate, universal, and initiated by a specific stimulus (e.g., peripheral flash). Conversely, endogenous selection of attention or orienting is influenced by an indi-

TABLE 9.1. Enns and Trick's (2006) Framework for Studying Selective Attention: "Four Modes of Selective Attention Including How It Is Acquired, What the Triggering Stimuli Are, the Degree of Conscious Control that Is Possible, and the Stability of Each Mode over Time"

Process	Origin	
	Exogenous (innate, hard-wired)	Endogenous (learned, acquired)
Automatic (unconscious)	<p>REFLEX (e.g., abrupt luminance transients and eye-gaze)</p> <ul style="list-style-type: none"> • Innately specified • Triggered by stimuli given priority by the nervous system • Unconscious, automatic, fast, obligatory, effortless • Avoided only with deliberation • Emerges on a developmental timetable • Stable once acquired (differs little across the lifespan or in special populations) 	<p>HABIT (e.g., words and symbols-arrows)</p> <ul style="list-style-type: none"> • Learned when goal repeated in specific environment • Triggered by stimuli associated with specific goals in past • Unconscious, automatic, fast, obligatory, effortless • Avoided only with deliberation • Can emerge at any time • Can fade or be replaced at any time; strength varies with practice
Controlled (conscious)	<p>EXPLORATION (e.g., pop-outs in visual search, change detection)</p> <ul style="list-style-type: none"> • Innately specifies generic goal for novel situations • Default mode for controlled processing • Conscious, controlled, slow, optional, effortful • Occurs when the only goal is exploration • Generic goal easily replicated by specific goal (switch to deliberation) 	<p>DELIBERATION (e.g., voluntary modulation when playing sports)</p> <ul style="list-style-type: none"> • Goal is internally generated and specific to the individual and context • Occurs when individuals are carrying out specific goals in a specific context • Conscious, controlled, slow, optional, effortful • Specific goals changed at will, but switches in goals take time • Needed to overcome unwanted automatic processes • Interferes with other deliberately selected goals

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vidual's goals and learning history. Based upon these two dimensions, four modes of visual selective attention are proposed (Table 9.1).

Although the Enns and Trick (2006) framework offers a more detailed manner of classifying selective attention responses, gaze cueing likely does not fall within one of their four modes. Enns and Trick denote selective attention to gaze cues as falling within the visual reflex category based upon the authors' interpretations of several social cueing studies (i.e., Friesen & Kingstone, 1998; Langton & Bruce, 1999; Langton et al., 2000). Designating gaze following as a reflex denotes it as innately specified and triggered by stimuli unconsciously, automatically, immediately, effortlessly, and in an obligatory fashion. Thus, according to Enns and Trick's classification, social orienting occurs in an analogous fashion to orienting to peripheral flash cues. However, as previously reviewed, evidence from spatial cueing tasks (e.g., Frischen, Bayliss, & Tipper, 2007; Frischen & Tipper, 2004; Gibson & Kingstone, 2006; Ristic & Kingstone, 2005; Vecera & Rizzo, 2006) indicates that social orienting is not "reflexive" in the traditional sense. Thus, an adapted framework is

TABLE 9.2. An Adapted Taxonomical System for the Aspects of Automatic Orienting of Visual Attention Consisting of Three Categories (Reflex, Social Orienting Response, Habit), Which Vary Along the Dimension of Origin

Exogenous ↔ Endogenous			
Automatic Orienting	REFLEX <ul style="list-style-type: none"> • Innately specified • Triggered by stimuli given priority by the nervous system • Unconscious, fast, obligatory, effortless • Avoided only with deliberation • Emerges on a developmental timetable • Stable once acquired (differs little across the lifespan or in special populations) 	SOCIAL ORIENTING RESPONSE <ul style="list-style-type: none"> • Innately primed but learned when repeated within dyadic social interactions • Triggered by stimuli (biological motion) given priority by the nervous system • Unconscious, fast, obligatory, effortless • Avoided only with deliberation • Emerges within the first few months of postnatal life but develops fully in first year • Likely stable across lifetime but more research is needed • May differ in special populations characterized by social deficits 	HABIT <ul style="list-style-type: none"> • Learned when goal repeated in specific environment • Triggered by stimuli associated with specific goals in past • Unconscious, fast, obligatory, effortless • Avoided only with deliberation • Can emerge at any time • Can fade or be replaced at any time; strength varies with practice
Examples of Cues	Abrupt luminance transients (flash cues), sudden appearances of stimuli	Eye-gaze (possibly: head turns, pointing cues, gross body movements, and tongue "pointing")	Arrows, words, learned directional symbols such as numbers and colors

required to adequately classify social orienting, and such a framework can be constructed based upon Enns and Trick's original work.

We present an adapted framework (Table 9.2) that consists of broad, conceptual categories that capture the important behavioral, neurological, and developmental differences between types of orienting responses. The term "social orienting response" aims to reflect the unique characteristics associated with orienting to eye-gaze and perhaps other directional and intentional body movements such as head turns and pointing.

For simplicity's sake, we address only the categories that reflect automatic orienting of visual attention and do not include Enns and Trick's (2006) second dimension of process (controlled orienting) within our framework because gaze cueing consistently elicits automatic orienting in typical populations. Thus, visual reflexes, the social orienting response, and visual habits are all automatic. These orienting responses are unconscious, fast, obligatory, effortless, and avoided only with deliberation. The categories discussed in our framework do vary, however, along the dimension of origin (from exogenous to endogenous), which reflects the degree to which the response is innate versus acquired through learning. For example, a visual reflex triggered by a flash cue is innately specified while a visual habit (triggered by an arrow) is learned based upon idiosyncratic environmental experiences (e.g., repeatedly seeing arrows as directional signs). The social orienting response is triggered by biological motion and biologically relevant species-specific social cues (e.g., eye-gaze, head turns, pointing cues, gross body movements, tongue "pointing") and falls between visual reflex and habit on the dimension of origin. Within this framework, the distinction between exogenous and endogenous orienting is not a dichotomy but rather a continuum that represents the degree to which a response is innate versus acquired through learning. For example, there is evidence that habits may lie on a spectrum, with arrows being more exogenous than other learned cues such as numbers and words (Fischer, Castel, Dodd, & Pratt, 2003; Hommel et al., 2001).

Neurological Findings: A Social Orienting Network

There appears to be some neurological evidence to support the notion of a unique "social orienting response" similar to that described by our proposed framework. In an effort to identify neural regions and a neural network that are unique to eye-gaze cues compared to the more traditional forms of exogenous and endogenous orienting, various neuroimaging techniques, including functional magnetic resonance imaging (fMRI), positron emission tomography (PET), electroencephalography/event-related potentials, and magnetoencephalography, have been used to identify the brain regions and attention pathways that are involved in social orienting. Certain brain regions have been highlighted as being critical to eye-gaze following and cueing, and these will be reviewed below. However, as will become apparent, none of these regions is unique to eye-gaze cueing; rather, most areas play a critical role

in traditional attentional models as well as many other aspects of human behavior. It seems possible that a specific network of brain regions elicited by gaze-cueing paradigms may be unique to gaze orienting as well as its developmental trajectory at the neural level. See Figure 9.2 for a graphical summary of theoretical brain networks associated with social orienting versus traditional orienting.

SUPERIOR TEMPORAL SULCUS

The superior temporal sulcus (STS) region has very commonly been identified as being a crucial brain region supporting gaze orienting. The STS has been defined as including the cortex within the STS, adjacent cortex on the surface of the superior and middle temporal gyri, and adjacent cortex on the surface of the angular gyrus (Allison, Puce, & McCarthy, 2000). Recent brain imaging research, including single-cell recordings in monkeys and neuroimaging in humans, has implicated the involvement of the STS region in the early analysis of biological movements (Pelphrey & Morris, 2006), including eye-gaze (Allison et al., 2000; Emery, 2000; Frischen, Bayliss, & Tipper, 2007). The STS is reportedly modulated by direct and averted eye-gaze (Calder et al., 2002; George, Driver, & Dolan, 2001; Wicker, Michel, Henaff, & Decety, 1998), and enhanced right STS activation for direct gaze (Pelphrey, Viola, & McCarthy, 2004), yet there is some evidence of greater response to averted gaze (Hoffman & Haxby, 2000). Birmingham and Kingstone (2009) have proposed that the STS is involved in the analysis of social information conveyed

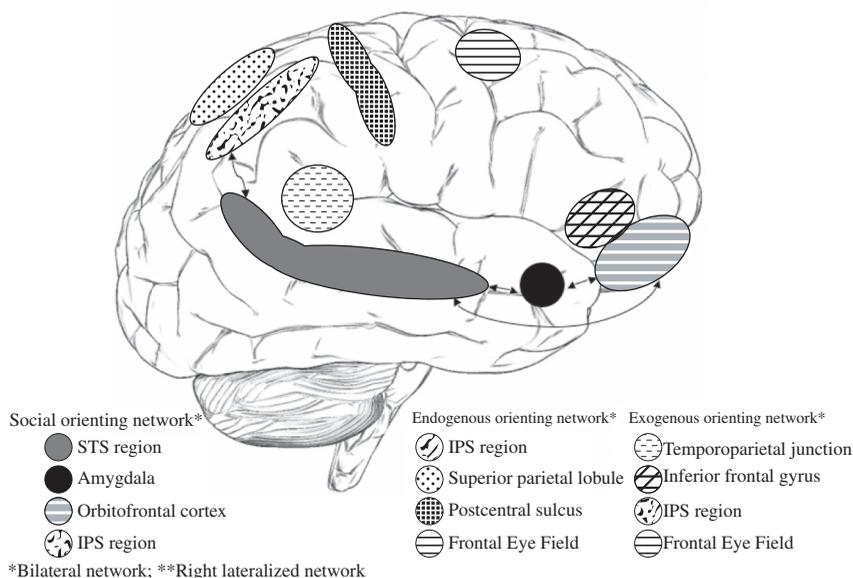


FIGURE 9.2. Theoretical model of the brain networks associated with endogenous orienting, exogenous orienting, and social orienting of attention.

by gaze direction and is most sensitive to gaze cues that are most meaningful. This notion is further supported by a study that highlighted the situational sensitivity of the STS by demonstrating that activation in the STS was significantly delayed when the eyes failed to provide meaningful information by looking away from the target compared to when the eyes provided relevant information by looking directly at the target (Pelphrey, Singerman, Allison, & McCarthy, 2003).

The STS has also been found to show enhanced activation in response to socially meaningful eye movement (Hoffman & Haxby, 2000; Hooker, Paller, Gitelman, Parrish, Mesulam, & Reber, 2003; Materna, Dicke, & Thier, 2008; Puce, Allison, Bentin, Gore, & McCarthy, 1998) and various other forms of biological movement (see Allison, Puce, & McCarthy, 2000, for a review), implicating the STS as having a role, more broadly, in social perception. Research has also suggested that the STS region is more generally tuned to stimuli that provide information about the actions or intentions of another person (Hoffman & Haxby, 2000; Kourtzi & Kanwisher, 2000; Senior et al., 2000). Thus, the findings implicate the STS as playing a role in the neural circuitry involved in gaze processing, specifically, as part of a neural system that develops sensitivity to biologically and socially meaningful cues such as eye-gaze over time.

INTRAPARIETAL SULCUS

Several studies of the brain regions involved in processing eye-gaze, including those that have employed PET (Wicker et al., 1998) and fMRI methodologies (Hoffman & Haxby, 2000; Pelphrey et al., 2003; Puce et al., 1998), have reported additional activation in the intraparietal sulcus (IPS) during passive eye-gaze viewing tasks. The role of the IPS in encoding spatial direction and mediating shifts of spatial attention in response to external directional cues (i.e., endogenous and exogenous attention) is well established. Materna et al. (2008) designed an fMRI study to examine whether the IPS was additionally implicated in eye-gaze processing or if its involvement was through its role in the spatial attention system in determining the direction of an individual's eye-gaze. In this study, participants were required to either follow the directional cue provided by the eyes of another person toward an object located in one of five possible locations in space, or make a nonsocially relevant judgment about the color of the iris. This study demonstrated that the IPS showed similar intensity of activation to both the socially and nonsocially relevant conditions and supported its role in encoding directional information and directing spatial attention, regardless of the type of stimulus cue (Materna et al., 2008).

AMYGDALA

The amygdala has long been implicated as having a role in processing socially relevant stimuli. It has traditionally been linked to processing stimuli that are emotionally arousing, especially fear, and more recently stimuli that are either aversive or

pleasant (see Adolphs, 1999, for more details). The amygdala has also been associated with playing a role in attaching meaning to socially salient cues (e.g., Allison, Puce, & McCarthy, 2000). This region may play a role in allocating resources to process biologically salient stimuli that require additional processing due to their ambiguity, regardless of the stimuli's emotional valence. Alternatively, the amygdala may be involved in attaching emotional salience to sensory input (Adolphs, 1999; Brothers, 1997).

Evidence has also been presented implicating the amygdala in gaze processing. For example, individuals with bilateral amygdala damage are impaired at identifying eye-gaze direction, whereas their ability to process direction from arrows is not (Young et al., 1995). Amygdala activation has been found in response to direct and averted gaze using PET, with a few studies indicating enhanced activation in the right amygdala in response to direct gaze (Wicker et al., 1998), bilateral activation in response to direct gaze, and enhanced activation in the left amygdala in response to gaze directed to another person (Kawashima et al., 1999). These findings suggest that the left amygdala may play a more general role in interpreting the direction of eye-gaze and that the right amygdala may be specifically involved in processing direct eye-gaze (Kawashima et al., 1999).

In contrast to the results reported by Wicker et al. (1998) and the conclusion drawn by Kawashima et al. (1999), another fMRI study reported less right amygdala activation in response to direct gaze as opposed to conditions in which the participants were awaiting direct gaze, perhaps indicating that increased activation is associated with circumstances in which one is awaiting such social contact (Hooker et al., 2003). Given these discrepancies, these results could mean that the amygdala's involvement in eye-gaze following may be influenced by situational demands.

FRONTAL LOBES

The involvement of the frontal cortex in social behavior is well established (Allison et al., 2000). The frontal cortices are considered important in interpreting complex social situations and in social perception by connecting decision making with social and emotional experiences (Adolphs, 1999; Damasio, 1994). There is extensive evidence from neuroimaging studies of frontal activation in gaze cueing tasks (Allison et al., 2000). A PET study first identified activation in the orbitofrontal cortex in response to mutual and averted gaze, but not when the stimulus eyes appeared to be closed (Wicker et al., 1998). Functional MRI studies have also shown evidence of activation in the right prefrontal regions and a ventral prefrontal region (Hooker et al., 2003) or right medial frontal gyrus (Tipper, Handy, Giesbrecht, & Kingstone, 2008) in response to gaze cues that provide socially relevant information, but not under conditions wherein the eye-gaze did not provide meaningful information (Hooker et al., 2003) or information was provided by an arrow cue (Tipper et al., 2008). Similarly, a recent event-related potentials study reported electrophysiological activity at fronto-central electrode sites in response to socially meaningful eye-

gaze cues, further implicating the frontal cortex in eye-gaze processing (Hietanen, Leppänen, Nummenmaa, & Astikainen, 2008).

These studies provide support for the involvement of frontal regions in the social orienting response. Based on more traditional cognitive accounts of the role of the frontal cortex as being one of decision making and planning, the above findings suggest that frontal cortices connect decision making with socially and emotionally meaningful experiences. It has also been proposed that the prefrontal cortex is involved in understanding another person's mental state (Hooker et al., 2003), which would make it an integral part of the neural circuitry of gaze processing.

A Distinct Neural Network for Social Orienting

Traditionally, neurophysiological models of attention have accounted for either exogenous or endogenous orienting, with little mention of orienting in response to social cues. Visual-spatial attention was thought to be controlled by two, partially separable, neural systems (e.g., Corbetta & Shulman, 2002). The first system processes unattended behaviorally relevant or salient stimuli and is right lateralized in the temporo-parietal and ventral frontal cortex. The second system, bilaterally located in the dorsal posterior parietal and frontal cortices, is involved in the cognitive selection of sensory information (Corbetta & Shulman, 2002). More specifically, exogenous (reflexive) attention is typically associated with a right ventral fronto-parietal network, recruiting the right temporo-parietal junction (including the inferior parietal lobule and the superior temporal gyrus), and the ventral frontal cortex (especially at the inferior and medial frontal gyri), the right frontal eye fields (FEF), and the right IPS. Endogenous (voluntary) attention modulates regions in the dorsal parietal cortex along the IPS, extending dorsomedially into the superior parietal lobule and anteriorly towards the frontal eye fields (see Corbetta & Shulman, 2002, for a review).

An extensive body of neuroimaging and electrophysiology research on the underlying neural mechanisms of attention in humans exists, but will not be reviewed here (see Corbetta & Shulman, 2002; Pelphrey, et al., 2004). Generally, many studies have concluded that the exogenous and endogenous attention systems are distinct yet overlapping, with endogenous attention tasks usually recruiting more brain areas than exogenous orienting tasks (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Culham et al., 1998; Kim et al., 1999; Lepsien & Pollmann, 2002; Mayer, Seidenberg, Dorflinger, & Roa, 2004; Nobre et al., 1997; Rosen et al., 1999). Similarly, evidence is mixed regarding distinct areas involved in processing eye-gaze cues. Many of the brain regions involved in processing biologically meaningful orienting cues, such as eye-gaze cues, seem to be distinct yet overlapping from those recruited to process non-biologically relevant attentional cues.

A hypothetical “social brain” in humans (e.g., Allison et al., 2000)—a three-part circuit responsible for understanding the intentions, attitudes, and feelings of other individuals (e.g., Baron-Cohen, 1995; Brothers, 1990)—has been proposed as a distinct neural network responsible for orienting in response to social cues. The hypothesized brain regions in this circuit, including the STS, the amygdala, and the orbitofrontal cortex, have been consistently identified in studies examining the neural regions involved in eye-gaze processing, prompting a few researchers to propose a neural circuit for social orienting that is distinct from circuits recruited for processing non-biologically relevant cues (Hietanen et al., 2006, 2008; Wicker et al., 1998). The social orienting system is thought to rely mainly on brain regions sensitive to the perception of eyes, eye-movement, and gaze direction, largely found in the STS (Akiyama et al., 2006; Allison et al., 2000).

The STS has reciprocal connections with many regions of the brain identified as being important in attributing meaning to eye-gaze, attributing meaning to complex social cues, and facilitating spatial direction. These regions of reciprocal connectivity include the amygdala (Allison et al., 2000; Frischen, Bayliss, & Tipper, 2007) and regions of the frontal cortices, especially the orbitofrontal cortex (Allison et al., 2000). The STS also has connections with the IPS, which, as previously discussed, is important for spatial processing and orienting attention (Frischen et al., 2007). Anatomically, the STS is well situated in the brain to integrate information from both the ventral “what” stream and the dorsal “where” visual stream (Allison et al., 2000; LaBar, Crupain, Voyvodic, & McCarthy, 2003). The ventral system, including the amygdala and regions of the frontal cortices, is traditionally associated with form recognition and object representation, and has also been implicated in processing static, emotional pictures (LaBar et al., 2003).

The evidence to support a social orienting system from lesion, neuroimaging, and electrophysiological studies is thus far equivocal. Many authors have found support for the notion of a partially segregated attentional system recruited by biologically relevant eye-gaze cues, whereas others have failed to identify a segregated system (see Birmingham & Kingstone, 2009). A handful of lesion studies have reported results that are consistent with separable attentional networks. Akiyama et al. (2006) found that orienting in response to an eye-gaze cue was disrupted whereas attentional orienting in response to an arrow cue remained intact in the case of a person with a lesion in the right superior temporal gyrus (part of the STS region). Similarly, patients with visuospatial neglect, who normally do not attend to half of their visual field, can follow eye-gaze and attend to their neglected field, but these patients do not orient to their neglected visual field when arrow cues are presented (Vuilleumier, 2002). Likewise, a study in split-brain patients demonstrated that arrow cues elicited activation in both hemispheres, whereas eye-gaze cues elicited activation only in the right hemisphere (Kingstone, Friesen, & Gazzaniga, 2000). Thus, following brain injury, different brain regions are recruited by eyes versus arrows and demonstrate different behavioral abilities with regards to social or non-social orienting. In contrast, a later study of a split-brain patient did not show this

lateralization of eye-gaze cues and instead reported bilateral activation in response to both types of cues (Ristic et al., 2002).

Results from neuroimaging are also equivocal. A recent review by Birmingham and Kingstone (2009) concluded that results generally do not support segregated attentional systems. However, a few imaging studies have reported results consistent with a distinct system. A PET study found that different neural regions were recruited in response to eye-gaze and arrow cues, with eye-gaze uniquely eliciting STS activation (Hooker et al., 2003). More recently, the brain regions mediated by shifts in attention triggered by gaze versus arrow cues were examined in an fMRI study (Hietanen et al., 2006). Gaze-cued orienting elicited activation in three focal regions in the left inferior occipital gyrus and right medial and inferior occipital gyrus. In contrast, arrow-cued orienting elicited a much broader network, including bilateral activations in the medial temporal gyrus and left IPS, as well as in the right FEF and supplementary eye fields (Hietanen et al., 2006). Similarly, an event-related potentials study compared orienting-related neural activity evoked by simple schematic gaze cues and arrow cues (Hietanen et al., 2008) and found that arrow cues elicited the posterior negativity over occipital-parietal channels that is typically reported in the literature (the early directing attention negativity [EDAN]), whereas eye cues did not. Likewise, arrow cues elicited a fronto-central negativity in the left hemisphere and eye-gaze cues did not (Hietanen et al., 2008). These results were again interpreted as providing support for a distinct social orienting neural network (see Fig. 9.2 for a graphical representation of these theoretical brain regions).

Birmingham and Kingstone (2009) proposed that differences in brain activation may not reflect distinct attentional networks but rather that different brain areas are recruited to process different stimulus types (i.e., visually analyzing an arrow vs. an eye) or that the context of the cues may contribute to different brain activations. In support of this hypothesis, they cite Tipper et al. (2008), who used the same stimuli for both the arrow and the eye-gaze conditions, simply instructing the participants to see the stimuli as an arrow or an eye, and did not find neural differences between the two conditions. Possibly, neural differences may reflect more familiarity with eyes than arrows, explaining why a few studies report more widely distributed networks for arrow cues than eye-gaze cues (Hietanen et al., 2003). This is similar to the “expertise hypothesis” in the face literature, which predicts that faces will elicit regions of the brain distinctly from other stimuli because humans are very familiar (i.e., experts) with faces (Tanaka, 2001).

Following from this, an appropriate approach to examining this hypothesis would be to look at the neural development of gaze orienting. In the face processing literature, it is well established that the brain’s response to faces changes across development, reaching adult levels sometime during late adolescence (Taylor, Batty, & Itier, 2004; Taylor, McCarthy, Saliba, & Degiovanni, 1999). These age-related changes likely reflect a human’s increasing familiarity and expertise with faces. Likewise, increased familiarity with eye-gaze, as reflected in the adult brain, would

likely look different in children and show a progression towards adult-like activations across development.

Developmental Findings: Emergence of the Social Orienting Responses

Automatic orienting to gaze does not appear *de novo*; there exists a developmental progression whereby environmental inputs interact with inborn perceptual biases. Neither a strong nativist view (e.g., the Eye Direction Detector; Baron-Cohen, 1995) nor Skinnerian conditioning fully accounts for the development of orienting to gaze (see also Meltzoff & Brooks, 2007). Newborns show a strong perceptual bias for eyes, likely due to the high visual contrast between the iris and sclera, and prefer faces with direct eye contact (Johnson & Farroni, 2007). Early gaze following emerges from mutual gaze and relies upon following the motion of pupils (Farroni et al., 2000). Farroni, Mansfield, Lai, and Johnson (2003) found that eye contact prior to the motion of the pupils was necessary for early gaze following. Throughout the first year of life, gaze following becomes increasingly automatic. By 3 months of age infants reliably follow an adult's gaze towards close targets in the visual field but not towards moving targets (D'Entremont, 2000). By 6 months of age, typically developing (TD) infants consistently react to shifts in gaze direction (D'Entremont, 2000; Hood et al., 1998; Symons, Hains, & Muir, 1998) but do not follow gaze to interesting events occurring outside their visual field (Corkum & Moore, 1995). Moore, Angelopoulos, and Bennett (1997) conducted a study on 9-month-old infants and found that those who had already developed gaze following could reliably follow static gaze. However, those infants who had not developed spontaneous gaze following required head motion in order to learn gaze following. Eight- to 12-month-old TD spontaneously follow gaze towards static and moving objects within and outside of their visual field (Corkum & Moore, 1998). Most infants demonstrate an adult-like orienting response by 14 months of age (Farroni et al., 2000). In sum, infants initially require eye contact and are then cued by motion of the pupils or head turns. Later, infants can reliably follow another's eyes, but only towards static objects that they can see. It is not until the end of the first year or beginning of the second year that a mature social orienting response is observed.

The notion that inborn biases interact with environmental input so that gaze following in infancy develops to approximate the mature response is consistent with our proposed conceptual framework for social orienting. According to our adapted framework, acquisition of social orienting requires more environmental input than visual reflexes but less than visual habits. Developmental findings suggest that gaze following is more innate than arrow or word following but perhaps less so than orienting to sudden-onset cues. Developmental observations also converge with the "Interactive Specialization" (IS) perspective within cognitive neuroscience that is used to explain the origins of the social brain network in humans (Johnson et al.,

2005) and can elucidate the development of neural specialization associated with the social orienting response. According to the IS perspective, brain regions become increasingly tuned to specific stimuli (e.g., an upright face) across development, and likewise specific types of information become more efficiently processed by a more specified neural network. This occurs across development through interactions with the environment and between brain regions (Johnson et al., 2005). The IS model is based on evidence that some cortical regions begin with poorly defined functions, such that they are partially activated in a wide range of different contexts and by different tasks, and later become fine-tuned to specific tasks. The IS model predicts that increasing specialization and more focal localization of cortical processes, such as following eye-gaze, would occur during development (Johnson & de Haan, 2006), resulting in faster, more accurate orienting to social cues in general. Thus, repeated events of orienting to gaze in early life likely drive the specialization in neurological networks. Certainly, changes in functional connectivity often occur as a result of selective attention (Büchel & Friston 2000). Johnson et al. (2005) suggest that as development unfolds, there is increased specialization with brain networks associated with processing social stimuli. For example, eye-gaze processing may originally share neural activation networks with face processing but dissociate during development (Johnson et al., 2005).

The Social Orienting Response in Atypical Development

Atypical development of the social orienting response and associated neural specialization may lead to variability in social ability over time. Persons with autism and those with schizophrenia share the problem of social disability yet have different underlying neurocognitive mechanisms and structures associated with specific psychopathological symptoms. Recent findings suggest that both groups may show variability in social orienting (Goldberg et al., 2008; Johnson et al., 2005; Langdon et al., 2006; Ristic et al., 2005; Senju, Tojo, Dairoku, & Hasagawa, 2004), suggesting that neurocognitive and neurological markers of the social orienting response could potentially provide indices for the etiology of social psychopathology.

THE SOCIAL ORIENTING RESPONSE IN AUTISM

Individuals with autism have difficulties with social perception and social attention (DSM-IV; APA, 1994). They also show diminished use of eye contact and eye-gaze to infer another individuals' intentions (e.g., Pelphrey et al., 2005) and engage in less joint attention (see also Mundy & Vaughan, 2002). There are numerous clinical, anecdotal, and empirical reports of the failure of young children with autism to consistently follow another's eye-gaze (e.g., Dawson et al., 1998, 2004; Swettenham et al., 1998; Zwaigenbaum et al., 2005). This impairment in gaze following specifically, and social orienting in general, is not attributable to problems

tracking line of sight: Children with autism can accurately track another person's averted eye-gaze towards objects in their visual environment (Leekam et al., 1997).

Because of observed differences in gaze following behavior, gaze cueing has been studied in persons with autism with general expectation of finding hypoactivation of the social orienting response. However, findings are mixed: some research groups have reported that orienting to gaze is less reflexive in children and adolescents with autism (Goldberg et al., 2008; Johnson et al., 2005; Ristic et al., 2005), other groups have reported intact or normative cueing (e.g., Chawarska, Klin, & Volkmar, 2003; DeJong, VanEngeland, Kemner, 2008; Kuhn et al., 2010; Kylliäinen & Hietanen, 2004; Rutherford & Krysko, 2008; Swettenham, Condie, Campbell, Milne, & Coleman, 2003; Uono et al., 2009), and still other groups have reported that subtle differences are evident under more stringent experimental conditions (counter-predictive) and when eyes are contrasted with arrow cues (Senju et al., 2004; Vlamings, Stauder, van Son, & Mottron, 2005). Discrepant findings may be due to inconsistencies between studies, such as differences in participant characteristics (e.g., developmental status, diagnosis, matching technique) or methodology (e.g., schematic vs. photorealistic stimuli, moving or stationary stimuli, experimental conditions, SOAs, dependent measures). Alternatively, mixed findings may reflect actual heterogeneity in orienting to gaze within individuals with autism spectrum disorders (e.g., some individuals with autism may demonstrate intact orienting to gaze in some conditions, whereas others show an alternative attentional response). A third possibility is that cueing paradigms are artificially simplistic and thus limit our ability to robustly detect differences in the social orienting response in autism.

There is some neurological evidence for hypoactivation of the social orienting response in autism (Kylliäinen et al., 2006; Pelphrey, Morris, & McCarthy, 2005). For example, Kylliäinen and colleagues found subtle differences at the neural level in response to direct versus averted gaze in individuals with autism using magnetoencephalography. This study required participants to indicate when two faces presented in sequence were matching. The eyes in the faces were either looking toward (mutual eye-gaze), down, or away (averted eye-gaze) from the participant. In TD children, averted eye-gaze elicited a strong right lateralized response at 245 ms over inferior occipito-temporal regions, whereas children with autism showed a weaker but slightly enhanced right lateralized response over the same scalp region (Kylliäinen et al., 2006). Overall results suggested that individuals with autism were recruiting different neural regions to process averted eye-gaze. Pelphrey, Morris, and McCarthy (2005) also found autism-specific differences using an event-related fMRI to examine the hypothesis that there would be distinct neural systems in response to eye-gaze in individuals with autism compared to TD participants. They used a task that required participants (TD individuals and high-functioning individuals with autism) to look at a small checkerboard that appeared and flickered in an animated character's visual field. On congruent trials, the character shifted her gaze toward the checkerboard and on incongruent trials she shifted her eyes toward empty space. In TD individuals, the posterior STS region, the superior temporal

gyrus, the middle temporal gyrus, the inferior parietal lobule, as well as the right middle frontal gyrus, the right precentral gyrus, and dorsal aspects of the cingulate gyrus, all responded more strongly to incongruent versus congruent trials. This was interpreted by the authors as reflecting the interpretation of the virtual person's intentions, which recruited additional processing when an "error" was committed by the virtual woman. In contrast, in individuals with autism, increased activation in response to incongruent trials was lateralized to the left inferior frontal gyrus and the right insular cortex, the right posterior middle temporal gyrus, and the left middle and inferior occipital gyri. Furthermore, activation in the STS was equally elicited by congruent and incongruent trials in individuals with autism. These results converge with some behavioral results to suggest that individuals with autism are recruiting a different neural network to process eye-gaze and infer information from gaze direction.

The Social Orienting Response in Schizophrenia

Schizophrenia is a neurological disorder that is partially characterized by disturbances in social functioning (DSM-IV; APA, 2000), which may be associated with abnormalities in the social orienting response. Several brain regions that play a role in the social orienting response have also been implicated with the neuropathology of schizophrenia. In particular, abnormalities in the superior temporal brain region (where the STS is located) have been identified in schizophrenic patients (e.g., Gur & Pearlson, 1993; McCarley et al., 1993; Zipursky et al., 1994), and behavioral reports of abnormal reactions to gaze also exist. For example, Rosse et al. (1994) found that patients with schizophrenia demonstrated a response bias toward perceiving others as looking at them when the other's eyes were actually slightly averted and, in fact, gaze was not direct. This response bias was particularly pronounced in patients with paranoid symptoms and may be associated with delusions that one is being intensely observed or scrutinized. However, findings are mixed, as other researchers have found normal functioning in the posterior STS region (Brunet, Sarfati, Hardy-Baylé, & Decety, 2003) and typical gaze discrimination (Franck et al., 2002).

Langdon et al. (2006) proposed that individuals with schizophrenia may possess a hyperactive social orienting response. They used a spatial cueing paradigm with a head turn cue (i.e., a woman's head looked down, then to the left or right) to measure automatic versus controlled orienting of social attention (Langdon et al., 2006). In their first experiment, Langdon et al. used a non-predictive condition in which cues were not generally predictive of target location. At the shortest SOA (100 ms), patients with schizophrenia but not controls were significantly faster at target detection on congruent trials versus incongruent trials, whereas participants in both groups demonstrated a congruency advantage at longer SOAs (300 ms, 800 ms). Previous findings have indicated that neuro-typical adults require at least 200- to 300-ms cue-to-target delays before head turn cues can reliably elicit facilitation effects (Driver et al., 1999; Langdon & Smith, 2005). Thus, the facilitation at 100 ms SOAs demonstrated by patients in Langdon et al.'s (2006) study suggests that

individuals with schizophrenia may be abnormally over-responsive to social cues. In a second experiment, Langdon et al. used a counter-predictive condition (cues were incongruent with target location on 80% of trials) in order to measure endogenous orienting of attention. Unlike control participants, patients with schizophrenia were not able to volitionally overcome the automatic congruency advantage elicited by the social cue (i.e., controls but not patients demonstrated faster RTs on incongruent trials at the 800-ms SOA). Thus, participants with schizophrenia demonstrated an impaired ability to volitionally overcome their social orienting response. Langdon et al. suggested that a hypersensitive social orienting response, coupled with difficulty making accurate inferences concerning other's intentions, may be associated with paranoid symptoms (i.e., distrust, vigilance, hyperarousal). At a neurological level, Langdon et al. postulate that "heightened amygdala activity that is associated with a heightened sense of personal emotional significance 'primes' the STS to detect signals of other people's intentionality in schizophrenia" (p. 427).

Autism and schizophrenia may serve as a viable test of the hypothesis that hypo- or hyper-activation of the social orienting response is related to general social ability. The available findings suggest that abnormal social orienting responses and atypical brain activation with regards to the social orienting neural network can both occur where compromised social functioning is present. The hyperactive social orienting response hypothesized in persons with schizophrenia by Langdon et al. (2006) contrasts with the hypoactive social orienting response hypothesized in persons with autism (Goldberg et al., 2008; Johnson et al., 2005; Ristic et al., 2005; Senju et al., 2004; Vlamings et al., 2005). Burns (2006) proposed that schizophrenia and autism are potentially related with regard to etiology because the central features of both disorders involve alterations in recently evolved human social behaviors. Biological theorists Crespi and Badcock elaborate on this view and argue that schizophrenia is associated with hypersensitivity to social cues and extreme inferences regarding social information, resulting in the over-attribution of mental states, whereas in autism there may be a diminished sensitivity to social cues, and social cognition is underdeveloped (Crespi & Badcock, 2008). In each case, orienting to social cues may be a critical skill that develops atypically and interferes with the "social opportunities" of children to engage in sharing attention with other meaningful people in their lives. In turn, diversity, or in some cases atypical social experience, would likely lead to variability in the development of social competence.

Concluding Remarks

We reviewed evidence from behavioral cueing, neuroimaging, and developmental literatures suggesting that orienting to social cues is a distinct form of visual-spatial orienting with a distinct neural network. Behavioral cueing findings suggest that orienting attention in response to gaze cues is more reflexive than responding to arrow cues, and the developmental literature suggests that early exposure to gaze

cues likely facilitates over-learning, which results in automaticity. Neuroimaging research supports the existence of an overlapping but distinct neural network that is responsible for the social orienting response. Since extant dichotomous attention taxonomies do not adequately capture the construct of social orienting, we proposed an adapted framework for conceptualizing social orienting that is more elaborate in classifying both the degree to which orienting is consciously controlled and the extent to which learning and experience plays a role in the acquisition of the orienting behavior. The proposed conceptual framework is consistent with a developmental systems theory with regard to explaining how child factors such as preferences for luminance contrasts, human faces, and moving stimuli interact dynamically with environmental factors to produce increased behavioral and neural specialization of the social orienting response. We presented the examples of autism and schizophrenia, disorders characterized in part by unusual social behavior, which have sometimes been found to be associated with either hypo- or hyperactive social orienting responses as well as atypical brain responses to averted gaze cues. Our goal in presenting an adapted framework is to help to clarify communication of research findings as well as highlight new areas for investigation. For example, the social orienting response can be studied across autism and schizophrenia, rather than independently within either highly heterogeneous disorder, with the goal of identifying commonly affected brain areas. Accordingly, the social orienting response may prove useful as an endophenotype (i.e., a simpler, more quantifiable, and reliable measure of a phenotype within a disorder) that has the power to identify the genetic underpinning of complex and heterogeneous psychopathologies and improve our understanding of typical and atypical human social development (see Iarocci, Yager, & Elfers, 2007).

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