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Mirroring, Mentalizing, and the Social Neuroscience of Listening

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Listening to another speak is a basic process in social cognition. In the social neurosciences, there are relatively few studies that directly bear on listening; however, numerous studies have investigated the neural bases of some of the likely constituents of successful listening. In this article, I review some of this work as it relates to listening, with a focus on two auxiliary processes in the comprehension of speech: perceiving the nonverbal behaviors, such as facial expression, that accompany an utterance (i.e., how it is being said); and interpreting an utterance and the nonverbal behaviors that accompany it in terms of the speaker’s state of mind (i.e., why it is being said). The review indicates the presence of two large-scale systems in the human brain that play a major role in successful listening: the putative mirror neuron system, which likely facilitates the relatively automatic perception of the how of speech; and the so-called mentalizing system, which likely underlies our ability to actively reach...
conclusions about the why of speech behavior. I conclude by considering the possibility that the dynamic interaction of mirroring and mentalizing processes may be pivotal for successful listening and social interaction more generally.

INTRODUCTION

Insofar as the human brain may have evolved its present form and function to meet the demands of the social world (Adolphs, 2009; Dunbar, 1993), it may not be a stretch to say that the brain is built for listening to others. In the past two decades or so, the rapid development of brain imaging techniques such as functional magnetic resonance imaging (fMRI) has made it possible to study the working brain as people perceive, think about, and interact with other people. In this article, my aim is to provide the reader with a brief overview of this work as it pertains to psychological theories of listening. In particular, I will focus on the studies investigating the neural bases of two social cognitive processes that, along with speech comprehension, likely play a major role in successful listening: perceiving the nonverbal behaviors, such as facial expression, that accompany an utterance (i.e., how it is being said) and interpreting an utterance and the nonverbal behaviors that accompany it in terms of the speaker’s state of mind (i.e., why it is being said).

This focus parallels the push in the development of listening theory to consider aspects of listening other than the mere comprehension and retention of what is being said (Bodie, 2012). For the sake of concreteness, I will begin with an example illustrating the difference among the what, how, and why of speech acts. Imagine you have just delivered a talk at a conference that advances theory X. A colleague of yours whom you know is critical of theory X approaches you and says, “I very much enjoyed your talk.” Here, what was said regards the denotative meaning of the utterance. To process the denotation of a statement, one simply recruits basic processes in language comprehension and perhaps also more general cognitive processes required for remembering the statement later. However, how it was said regards the perception of the nonverbal aspects of the voice in which it was said (e.g., intonation) and the nonoral motor behaviors that accompany it (e.g., facial expression, gesturing). It is easy to see that the meaning of the utterance can vary dramatically as a function of variability in how it was said: this can be as simple as the difference between a smile and a scowl. Finally, why it was said involves an inference about the speaker’s underlying state of mind (e.g., intent in saying that, attitude toward me and the talk). This distinction between how and why mirrors the distinction between bottom-up and top-down processing described by Edwards (2011), where how it was said involves encoding incoming stimulus information (e.g., intonation, facial expression) in bottom-up fashion, while why it was said requires the use of prior knowledge (e.g., this colleague doesn’t like theory X) and inferential rules (e.g., if a person says they like something and you believe they do not, they are probably being deceptive) to reach conclusions about stimuli in a top-down fashion (see Palomares, 2008).

In the first section of the article, I will briefly discuss the limitations of fMRI for studying complex psychological processes such as listening. In the next section, I will review research germane to characterizing the neural bases of comprehending how it is being said, with an emphasis on studies of perceiving and mirroring nonoral motor behaviors, such as actions and emotional expressions. Next, I will review research germane to characterizing the neural bases of comprehending why it is being said, with an emphasis on studies of mental state inference.
(mentalizing). Following this, I will consider the extent to which the interaction among brain systems for understanding how and why may be particularly important for successful listening.

RELEVANCE OF NEUROIMAGING RESEARCH FOR LISTENING THEORY

It is important at the outset to evaluate the relevance of neuroimaging research for listening theory. Here, I consider two basic questions that are central to such an evaluation: (1) To what extent has listening been the subject of investigation in existing neuroimaging studies of social cognition? (2) Even if listening (or listening-related phenomena) have been the subject of investigation, what could neuroimaging evidence contribute to psychological theories of listening? Given the known presence of a general neglect of the topic of listening in the social sciences (Bodie, 2011), it probably comes as no surprise that in the social neurosciences listening proper has not been an explicit topic of investigation. There are at least two reasons for this. The first is that, in principle, establishing a correlation between a mental process and brain function requires that the process of interest be well defined and capable of being validly and selectively manipulated in a brain imaging study. Whereas a process such as face perception fits this bill, a process as highly complex and currently lacking in theoretical specification as listening to another fits it much less so (see Bodie, Worthington, Imhof, & Cooper, 2008). The second reason is much more practical and regards the general difficulties, discussed at length by Zaki and Ochsner (2009), of studying high-level, naturalistic social cognition in neuroimaging experiments. To illustrate this, it will serve the reader to know what is required of participants in studies using fMRI, which is currently the most commonly employed neuroimaging technique. Participants in these studies are required to lie on a bed inside the narrow bore of a large piece of medical equipment (an MRI scanner), often for more than an hour. During this time, participants are asked to avoid moving their head at all costs, as head motion can corrupt the images produced by the scanner. During operation, the scanner is extremely noisy; hence, participants are required to wear earplugs, a fact that poses problems for researchers interested in presenting auditory stimuli to participants. To view the experiment, participants wear either video goggles or look at a mirror reflecting a rear projection. Given that speech produces head motion, behavioral measurements are typically limited to manual responses, a fact that poses problems for researchers interested in studying social interaction. Suffice to say, the methodological constraints of fMRI research presents a situation that is extremely low on what is traditionally termed mundane realism, or the extent to which the environment in which a psychological process is studied is similar to (or identical with) the environment in which that process typically occurs. Fortunately, fMRI studies fare somewhat better on psychological realism, or the extent to which the psychological experience induced during a study is similar to (or identical with) the psychological experience as it occurs in everyday life. However, when considering the complexities of the process of listening, which involves not only the perception and interpretation of an utterance but also the production of responses, it is unlikely that any fMRI study will fare well even in its level of psychological realism. Fortunately, the ecological validity of fMRI studies continues to improve as researchers move from studying simple social processes (e.g., face perception) to more complex social processes (e.g., the interpretation of facial expressions). Simultaneously, there is an upper limit on ecological validity simply due to the constraints of the method, and this should be kept in mind when evaluating the relevance of neuroimaging evidence for theories of highly complex psychological processes such as listening.
Hence, the review presented below is focused on characterizing the neural bases not of listening proper but of several listening-related phenomena.

The second question regards the theoretical contributions that brain imaging evidence is capable of making to listening theory. There are roughly two types of insights that neuroscience might offer (Henson, 2006). The first type, associations, occurs when two ostensibly unrelated processes are found to rely on a common neural substrate. This provides strong evidence that the two processes rely on a common mechanism. For example, Berger (2011) has recently discussed the implications for listening theory of a collection of brain regions in the human brain called the mirror neuron system (discussed further below). This system activates during both the production of a behavior, such as overt speech, as well as during the mere perception of the same behavior, such as watching another speak. Finding such an association lends support to the proposition that speaking and listening are not wholly separate but rely on an overlapping set of mental processes. The second type of evidence, dissociations, occurs when two ostensibly related processes are found to rely on dissociable neural substrates. As discussed below, work from our group has used this logic to establish that different modes of attending to the behavior of other people rely on starkly contrasting brain systems (e.g., Spunt & Lieberman, 2012a, 2012b). Such evidence can provide insight into theories attempting to divide and conquer a complex psychological process such as listening.

**HOW IS IT BEING SAID? MIRRORING THE SPEAKER**

The production of speech is an oral motor behavior accompanied by a variety of nonoral motor behaviors (i.e., facial expression, gesturing) that can augment, qualify, and, in some cases, completely contradict the meaning of what is being spoken. Put another way, the same statement can be made in different ways. Hence, in addition to the process of comprehending what others are literally saying (i.e., speech comprehension), any theory of listening must grapple with the complex process of comprehending how others are saying it (see Burleson, 2011).

Over the past two decades, neuroscientists have amassed a large amount of evidence demonstrating the brain is designed to rapidly process how others are behaving. Perhaps most specific to listening are investigations of voice perception, which have demonstrated highly selective neural responses to the sound of voices that are independent of linguistic content (Latinus & Belin, 2011). To give just one example, the temporal cortex, typically associated with language comprehension, houses regions which respond to human speech regardless of whether it is played forward or backward (Binder et al., 2000). These selective responses may be critical for extracting social and emotional information about the person speaking, that is, who is speaking and how they feel about what they are saying (Belin, Bestelmeyer, Latinus, & Watson, 2011).

Perhaps more surprising are studies demonstrating that the perception of nonverbal behavior, such as actions, symbolic gestures, and emotional facial expressions, activate the same regions of the brain involved in producing the same or similar behaviors. Collectively, these regions have come to be known as the mirror neuron system (MNS). Given the degree of influence the MNS idea has had in the social sciences, it seems useful to briefly review its history here. In the early 1990s, cellular recordings from the motor system of the macaque brain revealed neurons with the following property: they discharged not only if the monkey performed a grasping action (e.g., grasping a peanut) but also discharged when the monkey merely observed another monkey or
the experimenter performing the same action (di Pelligrino et al., 1992). It was as if the neuron mirrored the visual appearance of a grasping action. Subsequent studies helped constrain interpretation of the response of these mirror neurons. Gallese and colleagues (1996) showed that these neurons do not simply respond to the visual appearance of the goal-object (i.e., the sight of a peanut), nor do they respond to mimed actions (i.e., grasping a peanut in the absence of peanut). Umiltà and colleagues (2001) showed that a subset of these neurons respond to grasping actions even when the actual hand-object interaction is hidden from the monkey’s view, and this response only occurs when the monkey is led to believe the object is present. Even more remarkably, some mirror neurons appear to constrain their visual response based on the physical context of a motor action. Fogassi and colleagues (2005) mapped mirror cells that responded to grasping-to-eat but not grasping-to-place, as well as cells responding to grasping-to-place but not grasping-to-eat. As a final example, Kohler and colleagues (2002) identified so-called auditory mirror neurons that respond both to action production and to the mere sound of another performing the same action (e.g., the sound of tearing paper). These studies strongly suggest that these neurons represent an action in terms of the actor’s goal (e.g., pick up the peanut) and the intended outcome of that goal (e.g., eat the peanut).

Mirror neurons are believed to provide support for a theory of social cognition termed embodied simulation (Bastiaansen, Thioux, & Keysers, 2009; Gallese, 2007; Niedenthal, Mermillod, Maringer, & Hess, 2010). This theory begins with the observation that covert mental states (e.g., goals, emotions) are associated with overt motor behaviors. Given this, any mechanism that enables embodying the observable motor state of another (e.g., smile) can give us insight into their unobservable mental state (e.g., happiness). Mirror neurons offer a neurophysiological basis for this mechanism. Moreover, embodied simulation is consistent with a large body of behavioral work demonstrating that people spontaneously and rapidly mimic other people’s motor behaviors (Chartrand & Bargh, 1999; Dimberg, Thunberg, & Elmehed, 2000), and such mimicry, sometimes called the chameleon effect or motor contagion, has been shown to be causally associated with interpersonal rapport (Lakin & Chartrand, 2003) and with emotion recognition abilities (Neal & Chartrand, 2011).

It is important to note that the evidence for a human MNS is almost exclusively based on studies using techniques whose measures of brain activity reflect the activity of many millions of neurons rather than single neurons (but see Mukamel et al., 2010). Hence, the notion of mirror cells in the human brain has largely been replaced with that of a mirror neuron system, which has been demonstrated by showing that observed actions influence electrical activity in the motor system of the observer (e.g., Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) and that the patterns of brain activity that correspond to producing actions overlaps considerably with the patterns associated with merely observing actions (e.g., Buccino et al., 2001; Schippers et al., 2010). As recently discussed by Berger (2011), the MNS may play a key role in successful listening by providing a streamline from perception to action. Speech is itself a motor behavior, and in line with this there is evidence that the MNS participates in the production and perception of speech (Meister et al., 2007; D’Ausilio et al., 2009). Hence, the MNS may facilitate both the perception of speech acts by mirroring its motor correlates and in so doing facilitate the smooth performance of speech acts in response. In addition, the MNS is probably important for rapidly and automatically mirroring the how of speech acts. In two recent studies, we have shown that when an observer is explicitly directed to attend to how others are performing an action or expressing an emotion, the MNS is strongly and selectively active (Spunt & Lieberman, 2012a, 2012b).
of these studies (Spunt & Lieberman, 2012a), participants under fMRI viewed silent video clips in which professional actors made an emotional facial expression in response to something another person had said or done. Although the task of observing the clips tended to activate the MNS regardless of the observer’s goal, this activation was strongest when the observer was directed to attend to how the actor was showing their feelings. In this way, attending to and comprehending how likely involves mirroring processes in the MNS and may be a critical part of empathic understanding (Preston & De Waal, 2002; Zaki, Weber, Bolger, & Ochsner, 2009). Insofar as empathy is important part of being a good listener (Gearhart & Bodie, 2011) and being perceived as a good listener (Bodie, Cyr, Pence, Rold, & Honeycutt, 2012), this further underscores the likely importance of the mirroring processes for theories of listening.

**WHY WAS IT SAID, AND WHY IN THAT WAY? MENTALIZING THE SPEAKER**

Speech comprehension and the perception of para-linguistic cues such as the speaker’s vocal intonation and facial expression may both be important for successful listening, but they are often insufficient. This is because listening requires not simply a comprehension of what others are saying and how they are saying it, but also why they are saying it: what caused them to say that and to say it in that way? Utterances are typically designed to achieve a specific end, the speaker’s intent or goal, and can be used to infer the speaker’s underlying motives, beliefs, and dispositions (Palomares, 2008). Inferring these kinds of entities—mental states and dispositions—is often referred to as an act of mentalizing (Frith & Frith, 2006). In the social neurosciences, the discovery of mirror neurons is rivaled in importance by the discovery of a collection of regions in the human brain that reliably activate when individuals are prompted to think about the mental states of others (Frith & Frith, 2006; Saxe, 2006). For example, one of the first studies to identify this mentalizing system (MZS) found that it strongly responded when individuals were asked to judge whether someone with the knowledge of the historical figure Christopher Columbus would be able to infer the function of an object (e.g., a motor vehicle) by having access only to a photograph of it (Goel, Grafman, Sadata, & Hallett, 1995). This complex task requires suspending one’s own perspective (i.e., knowing what a motor vehicle is for) in order to represent the (potentially counterfactual) perspective of another (Leslie, 1987). This process of mentalizing is believed to rely on the presence of a theory of mind, evidenced by the ability to represent others as independent agents who act on the basis of their own mental representations of the world (Premack & Woodruff, 1978; Wimmer & Perner, 1983).

Mentalizing is likely a key component of the listening process, so much so that it may be necessary for participating in a conversation with another (de Gelder, 1987). When listening to others, verbal utterances and their nonverbal concomitants demand a great deal of active interpretation, a process which serves to provide the listener with an understanding of what the speaker intends to communicate, what they might be hiding, and generally, the beliefs, motives, and dispositions of the speaker which are implied by the message (Edwards, 1998; Happe, 1993; Palomares, 2008). Although the majority of neuroimaging of the MZS have not explicitly examined its role in the interpretation of verbal utterances, studies have suggested a critical role for this system in decoding the connotative aspects of messages, such as metaphor and sarcasm (Uchiyama et al., 2011) and indirect replies (Shibata et al., 2011). To give just one example, Shibata and colleagues (2011) had participants read vignettes in which one character asks another character a question...
(e.g., “What did you think of my talk?”) and compared the brain’s response to indirect replies (e.g., “It’s hard to give a good talk.”) to its response to direct replies (e.g., “I disliked your talk.”). Because indirect replies such as the one above are more ambiguous than direct replies, they require more active interpretation to reach a conclusion about the speaker’s intent. Compared to direct replies, indirect replies evoked significantly greater activity in the dorsomedial prefrontal cortex, a core region of the MZS. This demonstrates that the areas of the brain used to explicitly represent the mind of another are recruited in order to interpret the implied meaning of verbal utterances.

There is also evidence that the MZS is important for interpreting the meaning of nonverbal behavior. Areas of the MZS have been shown to respond during the observation of actions performed with deceptive intent (Grezes, Frith, & Passingham, 2004), during the observation of unusual actions (Brass, Schmitt, Spengler, & Gergely, 2007), and during the perception of the faces of known others (Gobbini & Haxby, 2007). In work from our lab, we have explicitly investigated the neural bases of the interpretation of nonverbal behavior by showing participants naturalistic videos of everyday actions and emotional facial expressions and asking them to explain why the behavior is occurring (Spunt & Lieberman, 2012a, 2012b; Spunt, Satpute, & Lieberman, 2011). Across several studies, we have shown that when comparing conditions where participants are merely asked to identify how the same behavior is occurring, inferring why selectively and strongly recruits the MZS. Although the majority of our studies have used silent videos lacking in verbal behavior, we have also shown the same effect when participants are asked to explain why for verbal descriptions of behavior. Taken together, these studies demonstrate that the MZS is involved in relatively stimulus-independent, top-down control of processes involved in the interpretation of both verbal and nonverbal behavior. Hence, in addition to the MNS, the MZS should be considered an important part of the listening brain.

THE COMPLEX RELATIONSHIP BETWEEN MIRRORING AND MENTALIZING

Given the complex nature of listening which likely involves processes subserved by both the MNS and MZS, it may come as a surprise that in addition to these two systems being anatomically independent, there is evidence that they are either functionally independent or even competitive. A recent meta-analysis of more than 220 neuroimaging studies of social cognition found that the two systems are rarely concurrently active and concluded that neither system aids or subserves the other (Van Overwalle & Baetens, 2009). This meta-analysis is generally consistent with studies demonstrating that during the perception of other peoples’ behavior, the two systems appear to process mutually exclusive types of social stimuli, with the MNS engaged by nonverbal, motor features and the MZS engaged by contextualizing verbal information (Waytz & Mitchell, 2011; Zaki, Hennigan, Weber, & Ochsner, 2010). Finally, there is evidence suggesting that under some conditions the two systems may actually interfere with one another. The two systems demonstrate anticorrelated activity when individuals are at rest (Fox et al., 2005), and other work suggests that areas of the MZS may operate to inhibit the tendency to imitate another’s action, a function putatively based in the MNS (Spengler, Cramon, & Brass, 2009).

This work suggests that under many conditions these two systems operate in a seesaw fashion: when one is strongly engaged the other is strongly disengaged. While it is still unclear what this seesaw relationship between the MNS and MZS means for human psychology, it has some
intriguing implications for theories of listening. For example, it suggests that when mentalizing a speaker we may necessarily have to temporarily disengage our attention from the dynamic inflow of sensory information (i.e., the perception of nonverbal behaviors and the comprehension of speech) that is critical for maintaining the social interaction. Such disengagement might have at least two negative results. One, such disengagement would likely interrupt auditory attention to speech, thus resulting in compromised comprehension of what the speaker is saying and ultimately in a breakdown of the social interaction. Insofar as such disengagement would likely produce a corollary disengagement of the MNS, a second negative result would be the reduction of processes putatively based in mirroring, such as motor mimicry. Given that mimicry is known to facilitate interpersonal rapport (Lakin & Chartrand, 2003), this would additionally compromise the interaction.

Contrary to evidence that the two systems are either independent or antithetical, a handful of studies suggest that under some conditions they may cooperate during social cognition (Zaki & Ochsner, 2012). Several studies have shown that the two systems exhibit concurrent activation during the observation of complex social stimuli (Brass et al., 2007; Iacoboni et al., 2004), especially when observers are explicitly induced to make judgments regarding the target’s internal state (Spunt et al., 2011). Another study demonstrated that activity in both systems positively predict the accuracy of observers’ ratings of another person’s emotional state (Zaki et al., 2009). Finally, several studies have now shown that the two systems may sometimes be functionally co-operative (e.g., Lombardo et al., 2010). Work from our lab has shown that in the specific case of mentalizing an observed emotional expression (Spunt & Lieberman, 2012a) or goal-directed action (Spunt & Lieberman, 2012b), the two systems may be part of a integrated functional sequence: the MNS may facilitate the identification of attribution-relevant motor events (e.g., picking up an object, smiling) while the MZS is primarily involved in attributing identified motor events to inferred social causes (e.g., the actor’s mental intent). Moreover, in a recent study we have provided evidence that as long as observers are actively attending to actions, the MNS is active even when the observer is performing a difficult, secondary mental task (holding in mind a phone number). On the other hand, the MZS is disrupted by the secondary mental task (Spunt & Lieberman, 2012c). This provides evidence for a dual-process model of the MNS and MZS, where the MNS efficiently encodes the how (and possibly also the what) of behavior while the MZS comes online only occasionally to figure out why. Generally, this underscores the validity of dual-process models of listening which identify which component processes may be more or less automatic and hence more or less influenced by extraneous interaction demands (Burleson, 2011; Edwards, 2011).

CONCLUSION

I have presented evidence for two large-scale systems in the brain that likely play a major role in successful listening. I have presented these systems as supporting two fundamentally different types of information-processing that likely make up successful listening. The first involves attention to the sensory and motor aspects of the other person’s verbal behavior, or to use colloquial language: how the other is saying it. This includes the perception of nonverbal aspects of the voice, such as emotional intonation, as well as the nonoral motor behaviors that typically accompany speech, namely, gestures and facial expressions. The second involves inferring the
implications of what was said and how it was said, a process that typically aims toward some representation of the speaker’s state of mind. As highlighted earlier, it is without a doubt that neuroimaging evidence is limited in its import for theories of listening. Indeed, it would not be an exaggeration to state that listening proper has not yet been examined using fMRI.

However, as experiments become more and more ecologically valid (e.g., Zaki & Ochsner, 2009) and as the brain systems supporting the component processes of listening become clearer, the utility of knowledge of the working brain for theories of listening should continue to grow. Of course, this will greatly depend on efforts by both listening researchers and social neuroscientists to find points of connection in both the language the two disciplines use to describe social interactions as well as the methods used to investigate it.

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