Who Goes There?

Minireview

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Our understanding of the visual system has benefited markedly from the hypothesis that visual processing occurs in two separate streams—one for what (or who) and one for where (Ungerleider and Mishkin, 1982). A *dorsal* processing stream mediates spatial processing through a circuit including the visual cortex (which contains the primary visual cortex and spatial processing areas, such as area MT) and the parietal cortex. A *ventral* processing stream mediates object processing through a circuit including the visual cortex (which contains the primary visual cortex and object processing areas, such as area V4) and the inferotemporal cortex. These two processing streams converge in the prefrontal cortex. However, in recent years, it has become clear that these two streams are not strictly parallel. For example, cells in the lateral intraparietal (LIP) area, an area associated traditionally with the dorsal stream, are also modulated by the shape of an object, a computation associated traditionally with the ventral stream (Sereno and Maunsell, 1998).

Recently, processing streams for audition, comparable to those in the visual system, have been proposed (Raushecker, 1998). In this model, a *dorsal* stream, which consists primarily of the auditory cortex, parietal cortex, and prefrontal cortex, processes information about the location of a sound source. A *ventral* stream, which consists primarily of the auditory cortex, the rostral superior temporal cortex, and prefrontal cortex, processes information about auditory objects. Given this interesting model, we think it is reasonable to ask how independent these two streams are. In this minireview, we will describe recent findings that probe the role of these different areas in spatial and object processing. Our focus will be on those studies that examine this cortical processing in areas beyond the primary auditory cortex in awake, behaving nonhuman primates with neurophysiological techniques or in humans with neuroimaging techniques.

Auditory Cortex

The nonhuman primate auditory cortex is organized into three distinct regions: the *core*, the *belt*, and the *parabelt*. Each of these three regions contains a number of anatomically and physiologically defined auditory fields; the primary auditory cortex is a tonotopic field in the core region of the auditory cortex. The details of the organization of the auditory cortex are out of the purview of this minireview, but the reader can refer to Kaas and Hackett (1998) and Rauschecker (1998) for further information on this topic.

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Information regarding sound source location and auditory identity is transformed between the core and noncore regions (Rauschecker, 1998; Rauschecker et al., 1999, Soc. Neurosci., abstract). For example, neurons in the belt region are more sharply tuned for sound source location than those in the core region. Similarly, neurons in the noncore regions of the auditory cortex respond preferentially to complex sounds (e.g., band-pass noise or species-specific vocalizations) relative to tones. In contrast, neurons in the core region respond preferentially to tones relative to complex sounds. It is important to note that neurons in the same noncore region can show comparable increases, relative to core regions, in their sensitivity both to sound source location and to complex sounds. Thus, while there is hierarchical processing between the core and belt regions, these areas do not process preferentially spatial- and object-related information.

Neuroimaging studies also indicate that in human auditory cortex the extent of activation within core and belt/parabelt regions increases as stimulus complexity increases (Wessinger et al., 1998, Soc. Neurosci., abstract). Activation for tones is primarily limited to the core regions. However, additional noncore regions are activated by more complex sounds such as band-pass noise bursts, frequency-modulated sweeps, and spoken syllables. Importantly, the same noncore regions are activated by speech-like stimuli and other complex sounds. This observation suggests that this hierarchical processing is *not* language specific but represents general processing necessary for the identification of complex sounds.

The role of the human auditory cortex in spatial processing is unclear. Some data indicate that the auditory cortex is not preferentially involved in spatial processing. For example, the activation in the auditory cortex is statistically similar when participants listen passively to sounds and when they actively localize sounds (Bushara et al., 1999; Weeks et al., 1999). Similarly, the auditory cortex is not modulated, relative to baseline controls, when participants listen passively to moving sound sources (i.e., auditory motion; Griffiths et al., 1998). In contrast, Baumgart et al. (1999) suggested that, in the posterior auditory cortex, there is preferential activation when subjects listen passively to auditory motion, relative to tasks in which they listen passively to stationary sound sources. These contrasting results may be due to differences in analysis techniques or methodologies. For example, the finding of Baumgart et al. (1999) may be due to their use of tonotopic organization to parcel auditory cortex into several functional regions of interest, which afforded them the ability to differentially probe the functional role of these regions.

Superior Temporal Cortex

The superior temporal cortex is important for auditory object processing. Lesions in the superior temporal cortex severely impair a monkey's performance on an auditory memory identification task (Colombo et al., 1996). Similarly, human neuroimaging studies have shown spreading activation to the superior temporal cortex

when subjects were asked to remember and to identify certain auditory stimuli (see Rauschecker, 1998). The role, if any, of the superior temporal cortex in spatial processing has not been determined.

Parietal Cortex

Neurons in the lateral intraparietal (LIP) area of the rhesus macaque are sensitive to the location of a sound source (Andersen et al., 1998; Grunewald et al., 1999). However, these neurons respond only to stimuli that are behaviorally relevant. Specifically, the activity of LIP neurons is modulated by sound sources when they indicate the future location of an eye movement. In this task, the sound is behaviorally relevant since the monkey is rewarded only when saccades are made to the remembered location of the sound. In contrast, the activity of LIP neurons is not modulated by sounds when presented in regions to which the monkey need not attend. In this task, the sounds are not behaviorally relevant since the monkey can ignore the sounds and still complete the task successfully. This observation is consistent with the notion that LIP activity does not reflect the physical characteristics of an auditory stimulus per se, as neurons in earlier parts of the auditory pathway may do, but instead reflects more abstract qualities of the stimulus such as oculomotor significance or motor planning.

Locating an object in space is not done by an anesthetized animal but by one able to locomote and move its head and eyes. A specific role for LIP in mediating eye movements is suggested by work examining the reference frame in which LIP activity is encoded (cf. Andersen et al., 1998). In these experiments, neural activity is recorded when monkeys make saccades to the remembered location of a sound source from different initial eye positions. In early parts of the auditory pathway, sound source location is based on interaural level and time differences and spectral cues and is consequently encoded in a head-centered reference frame. However, when monkeys make saccades to the remembered locations of sound sources, the response profiles of a large proportion of LIP neurons shift as a function of initial eye position. This shift is consistent with the notion that LIP neurons encode sound source location in an eye-centered reference frame; the remaining cells encode locations either in a head-centered reference frame or in an intermediate reference frame. The fact that there are head-centered, intermediate, and eye-centered neurons in area LIP suggests that it may be a locus of this transformation.

To our knowledge, there have not been any studies that have examined the role of the macaque parietal cortex in auditory object processing. However, since LIP neurons are involved in visual object processing (Sereno and Maunsell, 1998), it is reasonable to speculate that LIP neurons are also engaged in auditory object processing.

There is good evidence that the human parietal cortex is involved in auditory processing. For example, Weeks et al. (1999) demonstrated that the right inferior parietal lobule was activated to a greater degree during a memory localization task, which required a participant to compare the location of two consecutive sounds, than during a memory identification task, which required participants to compare the pitch of two consecutive sounds. In contrast, the left parietal lobule had a higher level of activation on the identification task than on the localization task. Interestingly, the inferior parietal lobule is also activated during visuospatial tasks, indicating that processing in this area is supramodal (Bushara et al., 1999). Others have shown that the right superior parietal lobule mediates both spatial and object processing (Zatorre et al., 1999). Finally, Griffiths et al. (1998) demonstrated that both the right and left superior and inferior parietal lobules were activated during passive listening to auditory motion. Together, these data suggest that the parietal cortex is involved in both spatial and object processing.

However, due to differences in experimental design, it is unclear whether the superior and inferior lobules contribute differentially to spatial and object processing or to perceptual and higher cognitive processing. For example, in the Griffiths et al. (1998) study, participants were instructed to listen passively to auditory motion. However, it may be possible they were also performing higher cognitive functions such as tracking the sound through covert eye movements. It has been shown that similar covert eye movements can activate parietal cortex in macaques (cf. Andersen et al., 1998). Thus, it is unclear whether parietal activation reflects motor planning or perception (Griffiths et al., 1998).

Prefrontal Cortex

The auditory spatial response properties of prefrontal neurons are comparable to those observed in area LIP. For example, neural activity in the prefrontal cortex is modulated by sounds that serve as a cue for future eye or limb movements; however, it is not modulated by sounds that are not behaviorally relevant (Vaadia, 1989; Russo and Bruce, 1994). In addition, neurons, at least in the frontal eye fields, encode sound source location in an eye-centered reference frame (Russo and Bruce, 1994). The functional similarities between neurons in area LIP and the prefrontal cortex may be due, in part, to the strong connections known to exist between these two cortical areas (Cavada and Goldman-Rakic, 1993). To date, there have not been studies designed to study auditory object processing in the prefrontal cortex in monkeys.

Neuroimaging studies have shown that the human prefrontal cortex is involved in both spatial (Griffiths et al., 1998; Bushara et al., 1999; Weeks et al., 1999) and object processing (Binder, 1997). Activity elicited during spatial processing most likely relates to eye-movement planning or other cognitive attributes associated with the stimulus and is not due to perceptual processing. Interestingly, the areas of the prefrontal cortex that are activated during auditory spatial tasks appear to be distinct from those activated during visuospatial tasks, suggesting modality-dependent processing of spatial attention (Bushara et al., 1999). Activity elicited during object processing has been documented using language studies. Many functional magnetic resonance imaging (fMRI) studies have demonstrated that speech and speech-like stimuli activate multiple prefrontal regions. Importantly, these regions of activation extend well beyond classic language areas in the inferior prefrontal cortex, supporting the notion that the prefrontal cortex is involved in aspects of object processing other than language.

Conclusion

Are there parallel processing streams for auditory spatial and object processing? At this point, the data do not adequately support this position. As we have discussed, auditory spatial and object processing appear to be mediated in the same cortical regions, which suggests that there are not independent processing streams. At best, studies have indicated that different cortical areas are involved preferentially in spatial or object processing (cf. Weeks et al., 1999). Of course, this may not be surprising, since most of the discussed cortical areas are strongly interconnected (Kaas and Hackett, 1998; Romanski et al., 1999). More experimentation is necessary to further specify the contribution of different cortical areas to spatial and object processing. For example, it will be important to determine whether, in the prefrontal and parietal cortices, there are distinct neuronal populations that separately mediate auditory spatial and object processing or whether the same neuronal populations can subserve both processes (Rao et al., 1997).

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