The Functional Specialization of the Planum Temporale

Zane Z. Zheng
Centre for Neuroscience Studies, Queen’s University, Kingston, Ontario, Canada

The planum temporale (PT) is an anatomically heterogeneous area with several architectonic subdivisions and extensive connections with other parts of the brain. Here I review a functional MRI study investigating the role of a functionally defined area (Spt) within the left PT in speech motor processing and discuss the functional properties of PT regions in the context of findings from recent neurophysiological and neuroimaging studies.

Functional organization of the planum temporale (PT) has been difficult to establish, due in large part to the lack of a precise definition regarding its anatomical boundaries and its remarkable morphological variability across individuals. Cytoarchitectonic studies in humans indicate that the PT, which is a triangular structure lying caudal to Heschl’s gyrus on the superior temporal plane, straddles at least four distinct cortical fields (internal: PaAi; external: PaAe; caudal–dorsal: PaAc/d; caudal–lateral: Tpt) that can be distinguished on the basis of their cortical laminar profiles (Galaburda and Sanides 1980). These fields exhibit a relatively lighter cell packing density and increased spacing between cell columns in thalamocortical and corticocortical input layers, compared with the primary auditory cortex (Sweet et al. 2005), and represent higher-order processing stages in the hierarchically organized auditory processing system. Despite the theoretical importance of understanding the roles that PT regions play in the auditory cortical processing, functional attributes of these regions still remain to be fully characterized.

Functional imaging studies of speech motor control suggest that the PT is engaged in mediating sensorimotor processes (Christoffels et al. 2007; Fu et al. 2006; Hashimoto and Sakai 2003; Tourville et al. 2008; Zheng et al. 2009). These studies explored the neural basis of auditory self-monitoring by comparing brain activation when auditory feedback was manipulated (either frequency shifted, or masked with noise, or delayed) with activation when auditory feedback was normal, during speech production. One common finding was an activation peak in the left posterior superior temporal gyrus or PT during perturbed auditory feedback, suggesting that the PT may be part of an on-line regulatory system that is critical for maintaining the fluency and reliability of speech. The fact that the activation was observed for manipulated speech only during production, but not during passive listening (Zheng et al. 2009), further suggests that the PT may be specifically involved in some aspect of speech motor processing. This view is well supported by anatomical studies demonstrating that there are multiple reciprocal connections between the posterior superior temporal regions and the frontal regions involved in vocal motor control, both in nonhuman primates (Petrides and Pandya 1988) and in humans (Schmahmann et al. 2007). These anatomical connections link putative auditory regions and motor regions, presumably facilitating rapid and robust information flow during speech motor processing.

Recent neuroimaging studies have directly assessed whether PT regions are recruited in sensorimotor processing during speech production (Buchsbaum et al. 2005; Hickok et al. 2003; Okada and Hickok 2006; Pa and Hickok 2008). The general approach adopted by these studies was to conduct a conjunction test with the activation patterns produced by the sensory (e.g., listening) and motor (e.g., vocalizing) conditions. The underlying assumption is that brain regions that are activated both during the perceptual condition and during the motor condition are involved in sensorimotor processing during speech. One functionally defined region (Spt) within the PT has been demonstrated to be consistently active during both sensory and motor conditions in these studies. One methodological problem with this approach is that it is difficult with functional magnetic resonance imaging (fMRI) to ascertain whether there is a common neural system or two functionally independent systems encoding the two different conditions in these functionally overlapping regions (Peelen and Downing 2006) and whether these activated regions are simply responding both to sensory and motor stimuli or whether they are integrating information from these two modalities.

The recent study by Hickok et al. (2009) in the Journal of Neurophysiology approaches this problem. Using fMRI procedures and multivoxel pattern analysis (Norman et al. 2006), the authors identified voxel-by-voxel activation patterns associated with sensory and motor aspects of speech processing in a region of interest (ROI) that has previously been shown to respond both to sensory and to motor conditions. They presented three experimental conditions (continuous speech; listen + rest; listen + rehearse) and a low-level rest condition in 15-s blocks (Hickok et al. 2009; their Fig. 1, http://jn.physiology.org/cgi/content/full/101/5/2725/F1). In the “continuous speech” condition, nonsense sentences were presented for the entire length of one block (15 s). In the other two conditions, sentences were presented for only the first 3 s followed by either “rest” or “covert rehearsal of the heard stimuli” (12 s) for the “listen + rest” and “listen + rehearse” conditions, respectively. The rationale for this experimental paradigm is that regions responsible for sensorimotor processing would be active both when “continuous speech” is compared with “rest” (sensory-dominant) and when “listen + rehearse” is compared with “listen + rest” (motor-dominant). Indeed, activation was observed in the ROI (Spt) in the left posterior PT in 14 of 22 subjects (Hickok et al. 2009; their Fig. 2, http://jn.physiology.org/cgi/content/full/101/5/2725/F2). Then the data from these 14 subjects were analyzed using a multivariate classification algorithm, in which each voxel in the ROI was assigned a weight according to how sensitive it was to a particular condition (either “continuous speech” or “listen + rehearse”). By judging the weight of each voxel in the time series, they were able to determine whether...
that voxel was more active during the sensory phase or the motor phase of the task.

In addition to the significant activation found in the Spt ROI for both sensory and motor conditions, consistent with their previous data (Buchsbaum et al. 2005; Hickok et al. 2003; Okada and Hickok 2006; Pa and Hickok 2008), the authors distinguished voxels that were preferentially responsive either to the perception of speech or to the production of speech (Hickok et al. 2009; their Fig. 5, http://jn.physiology.org/cgi/content/full/101/5/2725/F5). They found that the accuracy of their classification analysis was not significantly different from chance in the first 3 s, during which both “continuous speech” and “listen + rehearsal” conditions involved passive listening to sentences. However, after this point, the analysis began to separate the two types of voxels and yielded significant differences at the end of the time series, suggesting that it is the two functionally distinct conditions that led to this pattern of results. This finding is important in that it provides evidence for a functional distribution of subregions within the PT that may imply the existence of separate, functionally distinct populations of neurons that are preferentially responsive to either sensory or motor stimuli.

It is worth noting, however, that the location of Spt observed in the Hickok et al. (2009) study varies considerably among subjects (their Table 1). This raises the question as to whether the activation peaks in the Spt all correspond to the same cortical field or whether functional homogeneity across individuals is observed despite different neural systems being recruited in different individuals.

The observation of voxel-specific responses to either sensory or motor stimuli within the Spt by Hickok et al. (2009) can be viewed in the context of a substantial literature demonstrating multisensory convergence in low-level, unsensory auditory regions using neurophysiological recording and functional imaging techniques (Ghazanfar and Schroeder 2006; Schroeder and Foxe 2005). An early study using single-cell recordings in monkeys found that there were neurons in the Tpt (homologous to the caudal–lateral part of the human PT) responsive to auditory, somatosensory, and visual stimuli (Leinonen et al. 1980). More recent neurophysiological data have shown that neurons in both primary auditory cortex and more posterior belt areas exhibit enhanced firing at the single-unit (and multunit) level synchronized to either visual or somatosensory events that cue an auditory task, suggesting that auditory cortical neurons are capable of multimodal integration (Brosch et al. 2005). Experiments using multielectrode recordings revealed that somatosensory input evoked by median nerve stimulation elicits robust responses in the caudal–medial auditory belt cortex (CM) (Schroeder et al. 2001). Somatosensory responses in this CM region seem to be greater for the cutaneous stimulation directed toward the skin surface of the head and neck over other body parts, even at the single-neuron level (Fu et al. 2003). In addition, by simultaneously presenting auditory stimuli and tactile stimulation of body parts, integration of sound and touch was found on the lateral side of the caudal auditory belt cortex (CL) using high-resolution fMRI (Kayser et al. 2005). This region has also been suggested to integrate facial and vocal signals through the enhancement and suppression of local field potential activity (Ghazanfar et al. 2005). Somatosensory input to auditory cortical areas relies on their robust connections with insular regions, whereas visual input appears to come from other multisensory areas in the parietal cortex (area 7a) and the superior temporal sulcus (Tpo) (Smiley et al. 2007). The findings from the neurophysiological work in monkeys are also compatible with other functional imaging results in humans, since both audio-somatosensory (Dhanjal et al. 2008; Foxe et al. 2002; Schurmann et al. 2006) and audio-visual (Calvert et al. 1997; van Atteveldt et al. 2004) integration have been shown to occur in the left PT regions.

Therefore the current finding regarding the functional divergence within the Spt by Hickok et al. (2009) and the functional integration of various PT regions observed by other studies would appear to suggest that there are both unimodal (at least with respect to sensory and motor stimuli) and multimodal units within the PT.

Although Hickok et al. (2009) investigated the spatial patterns of response within a PT region under different conditions, the temporal dynamics of this region remain elusive. A number of studies have demonstrated that temporal patterns of neural activity in the auditory cortex may carry important information about functional significance. For example, it has been shown that transient and sustained neural responses are elicited in the primary and secondary auditory cortices, respectively, following the onset of the same auditory stimulus and these temporal patterns may reflect differences in the analysis of incoming auditory information (Seifritz et al. 2002). In line with this view, one study combining the use of fMRI and electroencephalography (Allmann et al. 2007) has revealed that auditory cortical neurons exhibit differential temporal patterns in response to the pattern changes and location changes in sound sequences presented, with slower and more sustained responses for the former and faster and more transient responses for the latter. In addition, based on the latency differences in the peak activity of neural response to acoustical changes, Schonwiesner et al. (2007) differentiated three stages of processing between the primary auditory cortex and the frontal cortex. Therefore it would be interesting to know what the temporal dynamics of the sensory-weighted and motor-weighted populations of neurons located within the Spt are and whether their temporal responses may give us more insight into the functional properties of PT regions.

In summary, Hickok et al. (2009) demonstrates subregions within an area (Spt) of the PT that are preferentially responsive to either sensory or motor stimuli, but that do not respond equally to both. This finding, together with a large body of previous studies on audio-motor, audio-somatosensory, and audio-visual integration, further adds to our understanding of the functional properties of an anatomically complex cortical area and lays a foundation for future exploration of sensorimotor processing in speech.

ACKNOWLEDGMENTS

I thank S. Lee for a critical reading of this manuscript and Prof. Greg Hickok, the leading and correspondence author of the study reviewed here, for helpful comments on an earlier version of this manuscript and for ensuring that the study is accurately represented in this commentary.

REFERENCES


