

# Chapter 12

## Redefining the Functional Organization of the Planum Temporale Region: Space, Objects, and Sensory–Motor Integration

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### 12.1 Introduction: Definitions, History, and Preview

The planum temporale (PT) is defined anatomically by the triangular surface on the supratemporal plane posterior to Heschl's gyrus (see Clarke and Morosan, Chapter 2). Its posterior boundary is the termination point of the Sylvian fissure, its medial boundary is the insula or the point where the supratemporal plane transitions into the parietal operculum, and its lateral boundary is the lateral lip of the superior temporal gyrus (Fig. 12.1).

Interest in the PT was promoted by the discovery of a left–right asymmetry in this structure, with the left PT being larger than the right in most (~65%) right-handed individuals (Geschwind & Levitsky, 1968). Given that the left PT comprises a part of classical Wernicke's area, the relatively larger size was thought to be an anatomical reflection of the region's functional specialization for speech processing.

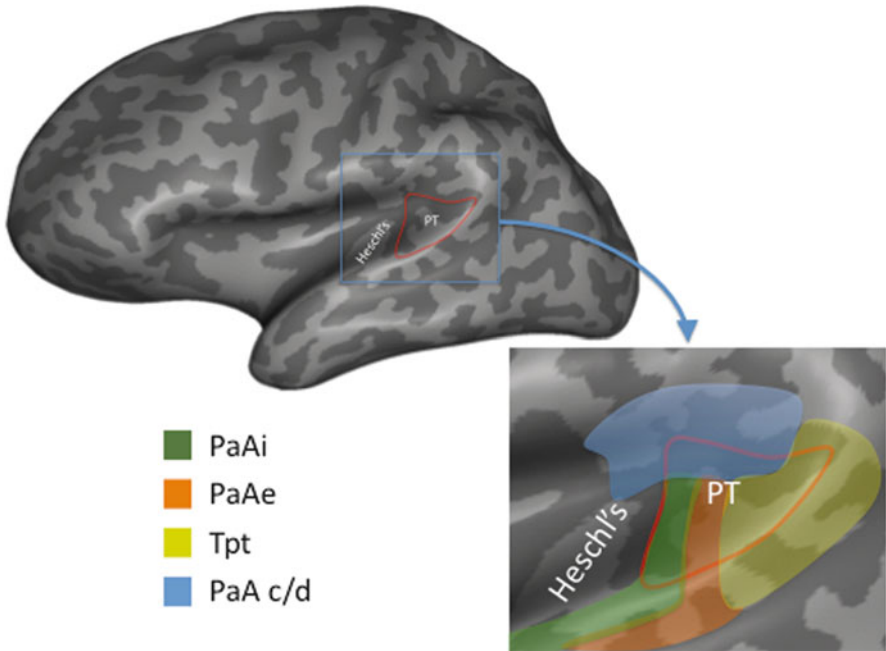
Several subsequent findings cast doubt on this view. One was that PT asymmetry was found to correlate with a nonspeech function, musical ability ( Schlaug et al., 1995). Another was that a similar leftward PT asymmetry was found in chimpanzees, a species without speech ability at all (Gannon et al., 1998; this of course questions the basis of the association with musical ability as well!). A third was that structural asymmetries of the PT did not correlate with language dominance as assessed directly using the intracarotid sodium amytal (Wada) procedure (Dorsaint-Pierre et al., 2006).

Results from functional imaging corroborated these findings. It was reported, for example, that the left PT responded equally well or even more robustly during processing of tone stimuli compared to speech (Binder et al., 1996; Hickok et al., 2003). In fact, a range of nonspeech signals were found to activate the PT including

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**Fig. 12.1** Location and cytoarchitectonic organization of the planum temporale. The location of the planum temporale on the posterior supratemporal plane is indicated in red outline on an inflated representation of the brain that shows structures buried in sulci and fissures. The inset shows a close up of the planum temporale region. Colors indicate approximate location of different cytoarchitectonic fields as delineated by Galaburda and Sanides (1980). Note that there are four different fields within the planum temporale, suggesting functional differentiation, and that these fields extend beyond the planum temporale. The area in yellow corresponds to cytoarchitectonic area Tpt which is not considered part of auditory cortex proper. Functional area Spt likely falls within cytoarchitectonic area Tpt, although this has never been directly demonstrated. PaAi, parakoniocortex — internal; PaAe, parakoniocortex — external; PaA c/d, parakoniocortex — caudodorsal Tpt, Temporal–parietal

multiple spatially dispersed sound sources (Zatorre et al., 2002; Smith et al., 2009), moving or spatially changing sound sources (Warren et al., 2002; Smith et al., 2004), visual speech (Calvert et al., 1997; Okada & Hickok, 2009), and auditory–motor integration (Buchsbaum et al., 2001; Wise et al., 2001; Hickok et al., 2003; Overath et al., 2007; Hickok et al., 2009).

This heterogeneity of function has led some authors to the view that the PT supports a general computation that operates over many classes of stimulus types. On one variant, the PT functions as a “computational hub” that takes as input a range of acoustic signals, performs a pattern matching operation, and then channels its output according to the nature of the signal; speech and other auditory objects would be channeled into one pathway, spatial information into another, and so on (Griffiths & Warren, 2002). According to another variant, which emphasizes auditory dorsal stream function (Rauschecker & Scott, 2009), the posterior superior temporal

region (which includes the PT) supports the implementation of “internal models,” mechanisms that model the input/output characteristics of the motor system for the purpose of motor control and/or sensory prediction (forward models). They argue for a “common computation mechanism” that implements internal models not just for speech as has been proposed previously (Guenther et al., 1998; van Wassenhove et al., 2005), but also for spatial hearing-related functions.

There is an alternative conceptualization of the PT, however. Although the computational hub hypothesis interprets the PT’s functional heterogeneity as evidence for some common computation that operates over a range of stimulus types and that characterizes the function of the whole structure, another possibility is that the PT’s heterogeneity of function is evidence for heterogeneity of function. That is, perhaps the PT is not functionally homogeneous but instead is composed of subfields that perform different operations, for example, spatial versus sensory–motor processes.

A terminological note: Although it is common to refer to the PT as if it were a functional region, this is misleading as functional boundaries do not respect gross anatomical boundaries. When referring specifically to the planum temporale as it is anatomically defined (e.g., if we are discussing previous studies that mapped the response patterns within this region), the term PT is used in this chapter. However, when referring to the broader functional–anatomic region, which likely spans portions of the parietal operculum, lateral portions of the superior temporal gyrus, and even the superior temporal sulcus, the term, *planum temporale region (PTR)* is used here.

## 12.2 Cytoarchitectonics of the Planum Temporale Region

Cytoarchitectonic studies of human auditory cortex demonstrate that several subregions exist within the PT and that the boundaries of these cytoarchitectonic fields extend beyond the gross anatomical boundaries of the PT (Fig. 12.1, see also Clarke and Morosan, Chapter 2). Galaburda and Sanides (Galaburda & Sanides, 1980) identified four areas that are at least partly within the PT. Three are classified as parakoniocortex, cortical fields with prominent granularity in layer IV and relatively sparse layer V, but to a lesser degree than the extremely granular konio fields, which are found on Heschl’s gyrus. PaAi (parakoniocortex—internal) is just lateral/posterior to Heschl’s gyrus and corresponds to the lateral belt region; PaAe (parakoniocortex—external) is lateral/posterior to PaAi and corresponds to the parabelt region; PaA c/d (parakoniocortex—caudodorsal) is caudodorsal to Heschl’s gyrus. The fourth area, Tpt (temporal–parietal), which occupies much of the posterior portion of the PT, has a weak layer IV and more prominent layer V and so is not classified as parakoniocortex. Galaburda and Sanides emphasize that Tpt “lacks specialty features of sensory cortex” (p. 609) and so should not be considered part of auditory cortex. This conclusion is reinforced by comparative studies that indicate that the homologous area in monkey, also called Tpt, is not considered part of auditory cortex (Sweet et al., 2005; Smiley et al., 2007). Interestingly, much of the anatomical asymmetry in the PT appears to be found in Tpt (Galaburda & Sanides,

1980). As is clear from Fig. 12.1, each of these regions extend well beyond the boundaries of the PT to include portions of the superior temporal sulcus, parietal operculum, and even supramarginal gyrus. A similar organization of the human PT was reported by Sweet et al. using other histological stains (Sweet et al., 2005).

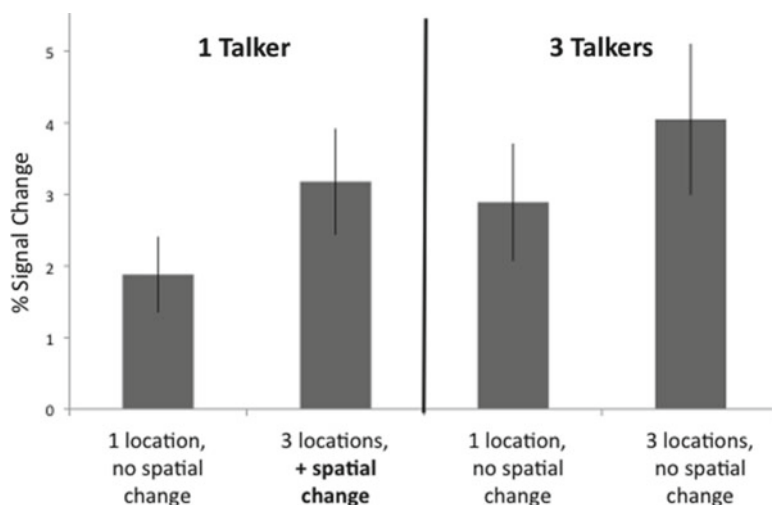
These findings indicate that the PT (and more broadly, the PTR) is anatomically heterogeneous, including belt and parabelt auditory fields, as well as an area, Tpt, which cannot be characterized as auditory cortex.

### 12.3 Role of the PT in Auditory Space and Object Processing

Portions of the PT have been found to respond to spatial auditory signals including moving sound sources (Baumgart et al., 1999; Warren et al., 2002; Smith et al., 2004) and nonmoving but spatially varying sounds (Warren & Griffiths, 2003; Smith et al., 2004; Smith et al., 2007). Several studies have assessed the relative selectivity of these spatial responses. One line of studies investigated whether responses in the PT were motion selective by contrasting moving sounds with sound sources that are perceived to jump from one location to the next (spatial change but without perceived motion). Two studies found the same degree of activation in the PT for both conditions, arguing against the view that the PT contains a motion-dedicated cortical region, analogous to visual area MT (Smith et al., 2004, 2007).

Another line of studies assessed the relative spatial selectivity of PT responses compared to nonspatial signals such as pitch or environmental sounds. This work has shown convincingly that sequences of spatially varying sound sources (changes in the location) yield greater activity in the PT than sequences of non-spatial variation (e.g., changes in pitch); the latter produce greater activation in Heschl's gyrus and more anterior auditory fields (Warren & Griffiths, 2003; Barrett & Hall, 2006; Altmann et al., 2007). Observations such as these have been used to argue for the existence of anterior “what” and posterior “where” pathways in human auditory cortex with the PT a major structure in the “where” pathway (Warren & Griffiths, 2003; Altmann et al., 2007; Rauschecker & Scott, 2009).

But other studies have cast doubt on the idea of a pure “where” function within the PT, or anywhere in cortex. Use PET, Zatorre et al. (2002), for example, found that increasing the number of sound source locations correlated with PT activity only when spatial information was useful for auditory object segregation. Specifically, presenting a noise stimulus at 1, 2, 3, 4, or 6 locations (in sequence) did not correlate with changes in PT activity, but presenting a set of 12 environmental sounds *simultaneously* at either 1 location or distributed over 2, 3, 4, or 6 locations did correlate positively with PT activity (Zatorre et al., 2002). As noted in the preceding text, however, other studies have reported a modulation of PT activity with spatial manipulations alone, which appears to contradict the result of Zatorre et al.. A more recent study using functional magnetic resonance imaging (fMRI; Smith et al., 2009) clarified the situation. This study manipulated the number of auditory objects, in this case with speech stimuli (1 vs. 3 talkers), and the number of spatial locations at which the stimuli



**Fig. 12.2** FMRI signal change in a region of interest (ROI) in the human planum temporale defined by a spatial manipulation. The ROI was defined by contrasting a spatial change (a single talker’s voice that bounced between three spatial locations) with a no-spatial change condition (a single talker’s voice that was stationary at one spatial location). The spatial effect is evident in the left two bars with spatial change eliciting more activity than no spatial change; this is the standard effect observed in the PT. Note, however, equal or greater signal amplitude is observed with no spatial change, that is, by simply adding talkers either in one location or in three different (static) locations. (Adapted from Smith et al., 2009.)

were presented (1 vs. 3 locations). Consistent with previous reports of “pure” spatial effects, presenting a single speech stimulus (talker) from one location yielded less activation than a single speech stimulus that bounced between three locations (Fig. 12.2, left half of graph). Spatial variation clearly modulated the response of the PT. However, simply adding talkers to the speech stream (three talkers presented simultaneously at one location) resulted in a similar increase in activity level in the PT (cf. middle two bars in Fig. 12.2). Finally, presenting three talkers simultaneously at three locations, *without spatial change*, resulted in the highest activity level (Fig. 12.2, right most bar). Thus, spatial change alone can modulate PT activity, but, consistent with the finding of Zatorre et al. the response in this region is particularly sensitive to the interaction of spatial and auditory object manipulations. As Zatorre et al. suggested, this finding is consistent with the proposal that portions of the PT are involved in auditory stream segregation and may use spatial cues in this service (Zatorre et al., 2002; Smith et al., 2009). On this view, there is no dedicated “where” stream in auditory cortex and “spatial” responses reflect a spatial *contribution* to some other computation (Middlebrooks, 2002). See also later.

In sum, although there is ample evidence that portions of the PT respond to spatial manipulations, there is no evidence to date suggesting that the PT contains a region dedicated to computing spatial location and/or auditory motion. Instead, spatial responses may reflect the *use* of spatial information for other functions.

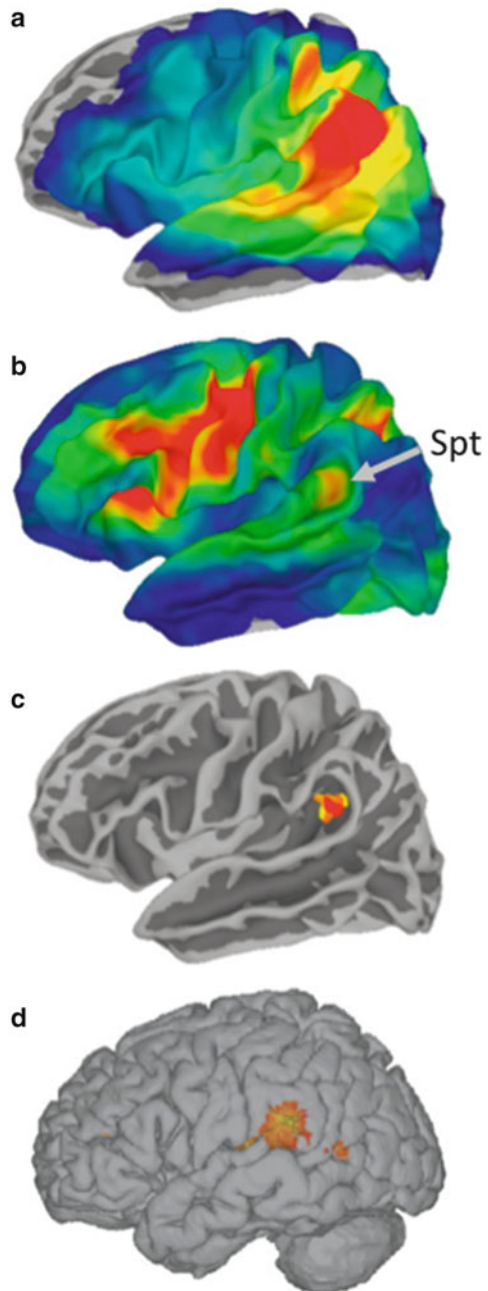
## 12.4 Role of the PTR in Auditory–Motor Integration

Auditory–motor integration is critical for several aspects of speech and auditory processing. In the speech domain, it is well documented that auditory feedback has relatively rapid (~100 ms) effects on speech production, for example, the disruptive effects of delayed auditory feedback (Yates, 1963; Stuart et al., 2002) and the pitch- or F1-shift reflex (Burnett et al., 1998; Houde & Jordan, 1998; Tourville et al., 2008). Auditory–motor integration is also critical in development where the young child must use auditory information in his or her linguistic environment to guide articulatory processes that are aimed at reproducing those sounds with the vocal tract (Hickok & Poeppel, 2000, 2004, 2007). This requirement extends to the suprasegmental domain: not only does one have to learn how to produce the individual sounds of the language, but also the sequences of sounds and syllables that correspond to the words of the language (Hickok & Poeppel, 2007). The ability to reproduce nonlinguistic sounds and sequences with the vocal tract (e.g., a dog’s bark or a melody) demonstrates that auditory–motor integration is not restricted to the speech domain.

Several lines of evidence link auditory–motor integration with the left posterior PTR. Damage to this area is associated with conduction aphasia (Fig. 12.3A) (Buchsbaum et al., e-pub 2011), a syndrome that results in a speech *production* deficit in which a patient’s speech output is fluent but marked by abundant phonemic errors in spontaneous speech (Benson et al., 1973; Goodglass, 1992). Conduction aphasics also have difficulty with verbatim repetition of speech, which is exacerbated when speech has little semantic content (Goodglass, 1992). Receptive speech abilities are largely preserved however, even for speech they cannot repeat (Baldo et al., 2008). The preserved receptive speech and fluent speech output suggest that the deficit in conduction aphasia involves neither acoustic perception nor motor execution of speech, but rather the interface of these two systems (Hickok et al., 2011; Buchsbaum et al., e-pub 2011). Direct cortical stimulation of the PTR has been reported to induce symptoms of conduction aphasia (Anderson et al., 1999).

Functional imaging studies of auditory–motor tasks have similarly implicated the left posterior PTR (Buchsbaum et al., 2001; Wise et al., 2001; Hickok et al., 2009). A series of studies have identified a set of cortical areas that have auditory–motor response properties, responding both during the perception and production of speech in verbatim repetition tasks (covert, i.e., subvocal speech is used in these studies to eliminate the auditory response to hearing one’s own voice during repetition) (Paus et al., 1996; Hickok et al., 2003; Hickok et al., 2009). The auditory–motor network identified by these studies includes posterior frontal regions (pars opercularis/area 44 of Broca’s area as well as more dorsal premotor regions), the superior temporal sulcus bilaterally, and the left posterior PTR (Fig. 12.3B). This posterior PTR activation likely falls within the distribution of cytoarchitectonic area Tpt but appears to be quite focal in most individuals and therefore probably comprises a subset of Tpt. This functionally defined area in the posterior PTR has been termed Spt (Sylvian–parietal–temporal) to distinguish it from the anatomically

**Fig. 12.3** (a) Distribution of lesions associated with conduction aphasia ( $n = 16$ ). Warmer colors indicate greater overlap. (b) Location of area Spt as identified in a listen and rehearse fMRI paradigm ( $n = 106$ ). (c) Overlap between maximal density of lesions associated with conduction aphasia and fMRI localization of Spt. (a–c from Buchsbaum et al., 2011). (d) fMRI localization of the effect of altered auditory feedback minus unaltered feedback. (Adapted from Tourville et al., 2008.)



defined area Tpt (Hickok et al., 2003). As Spt is strongly left dominant, it is worth noting again that of the cytoarchitectonic areas in the PT, Tpt exhibits the greatest degree of leftward asymmetry (Galaburda et al., 1978; Galaburda & Sanides, 1980), further reinforcing the link between Spt and Tpt. The location of Spt appears to overlap substantially with the region most consistently damaged in conduction aphasia (Fig. 12.3C) (Buchsbaum et al., e-pub 2011).

Beyond auditory–motor response properties, Spt exhibits several features characteristic of sensory–motor integration areas that have been identified in monkey parietal cortex (Andersen, 1997; Colby & Goldberg, 1999). For example, Spt appears to have both sensory-weighted and motor-weighted cell populations as evidenced by multivariate pattern analysis of fMRI data that has found distinguishable patterns of activity within Spt during the sensory and motor phases of a sensory–motor task (Hickok et al., 2009). Spt is not speech specific, responding equally well during the perception and covert production (humming) of melodic tone sequences (Hickok et al., 2003). However, like sensory–motor areas in the monkey parietal lobe, Spt does show motor effector specificity, responding more when the motor task involves the vocal tract (humming) than when it involves the manual articulators (imagined piano playing) despite identical sensory input (Pa & Hickok, 2008). This collection of observations has led to the proposal that Spt, rather than being an *auditory*–motor interface area, is a *sensory*–motor interface area for the vocal tract effector system (Pa & Hickok, 2008; Hickok et al., 2009). This is consistent with Spt’s presumed location within nonauditory area Tpt. It is also relevant in this context that area Tpt is substantially more developed in humans than in monkeys (Galaburda et al., 1978). This may reflect the dramatically increased load on sensory–motor coordination of vocal tract actions with the evolution of speech.

The aforementioned studies utilize sequences of sounds to study auditory–motor interaction. At least one study (Tourville et al., 2008) used an altered auditory feedback paradigm in which subjects phonated a vowel under conditions of normal or altered feedback (F1 shift). An activation focus was found in the PTR that responded more during altered than unaltered feedback (Fig. 12.3D) suggesting that this region supports sensory–auditory–motor interaction on multiple scales, that is, both at the level of phonetic features and sound sequences. It is an open question whether these levels rely on the same computational network or on parallel circuits.

Spt has been characterized as an auditory–motor integration area, but what does this mean computationally? There are two hypotheses. One is that the region that includes Spt, as well as the STG more broadly, comprises an auditory target map that compares the predicted auditory consequences of a speech act (a forward prediction) with the actual auditory feedback and generates an error signal in cases of mismatch (Golfinopoulos et al., 2010). Evidence for this view comes from the observation that the STG, including PTR, is more strongly activated when the subject’s speech output is altered compared to when it is not (Christoffels et al., 2007; Tourville et al., 2008; Takaso et al., 2010). Another possibility, hypothesized to hold of Spt specifically, is that it is performing a coordinate transform between auditory-based representations and a motor-based representations of speech (Hickok et al., 2009, 2011). Evidence for this claim comes from neuropsychology: the pattern of



sparing and loss in conduction aphasia has been characterized as a disconnection between intact auditory and motor speech systems (Jacquemot et al., 2007; Buchsbaum et al., e-pub 2011) and the lesions in this syndrome implicate Spt (Buchsbaum et al., e-pub 2011)

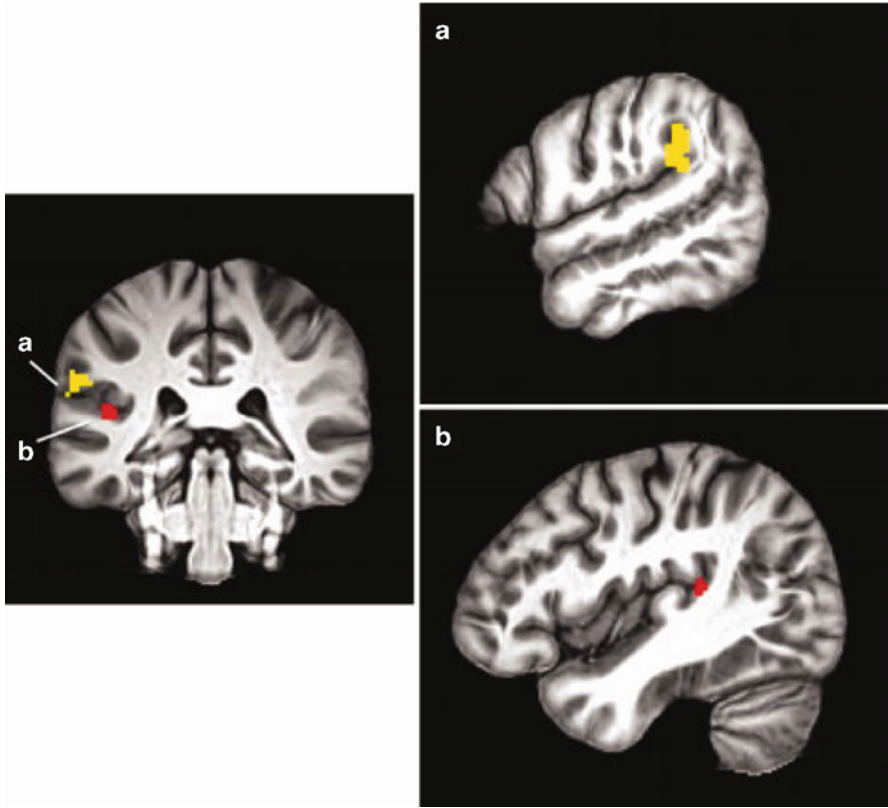
## 12.5 Functional Subdivision of the PTR into Auditory versus Sensory–Motor Function

It has recently been proposed (Hickok, 2009) that the PT is subdivided—or more accurately, the PTR—into at least two broad regions, an anterior sector that corresponds to unimodal auditory cortex and a posterior sector, area Tpt, that is more multimodal (Hackett et al., 2007; Zheng et al., 2009,) including a region, Spt, that specifically supports sensory–motor integration for vocal tract actions (Hickok et al., 2009). The cytoarchitectonic data reviewed in the preceding text supports this view in that the anterior portion of the PT has been classified as unimodal auditory cortex, whereas the posterior sector, area Tpt, lacks the defining features of sensory cortex. It does share some similarities, however, with area 44 (the pars opercularis) in Broca’s region. As Galaburda puts it, Tpt.”..exhibits a degree of specialization like that of Area 44 in Broca’s region. ... Thus 44 and Tpt are equivalent transitional areas between the paramotor and the generalized cortices of the prefrontal area, and between parakonio-cortex and temporoparietal occipital junction areas respectively. ...the intimate relationship and similar evolutionary status of Areas 44 and Tpt allows for a certain functional overlap.” (Galaburda, 1982, pp. 442–443). As noted previously, area 44 is part of the sensory–motor integration circuit that includes Spt in the posterior PTR. These findings are consistent with the view that the posterior PTR supports sensory–motor functions and is distinct from more anterior fields in the PTR.

Given this anatomical distinction, one wonders whether the spatial-related functions associated with the PT involve more anterior regions than the sensory–motor functions. A recent within-subject fMRI study addressed this question directly (Isenberg et al., 2011). This study employed a sensory–motor task (speech shadowing: immediately repeating back heard speech) as well as an auditory motion condition. In both individual-subject analyses and in the averaged group data, the activations for the sensory–motor and auditory motion conditions were distinct and in posterior versus anterior regions of the PT, respectively (Fig. 12.4).

### 12.5.1 *The PTR in the Context of the Dorsal and Ventral Auditory Streams*

There is convergence on the view that the PT is part of the auditory dorsal stream (Warren et al., 2005; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009) but less consensus regarding its function. The dominant competing theories are the



**Fig. 12.4** fMRI activation for sensory-motor task is shown in yellow (a) and the spatial hearing manipulation is shown in red (b). Adapted from Isenberg et al., 2011.)

sensory-motor theory (Hickok & Poeppel, 2007) and the spatial “where” theory (Rauschecker, 1998; Rauschecker & Scott, 2009). In previous sections we summarized the evidence for the sensory-motor theory as well as the evidence for and against a pure “where” theory. Here we describe a reinterpretation of the notion of sensory processing streams motivated in part by the functionally subdivided model of the PT.

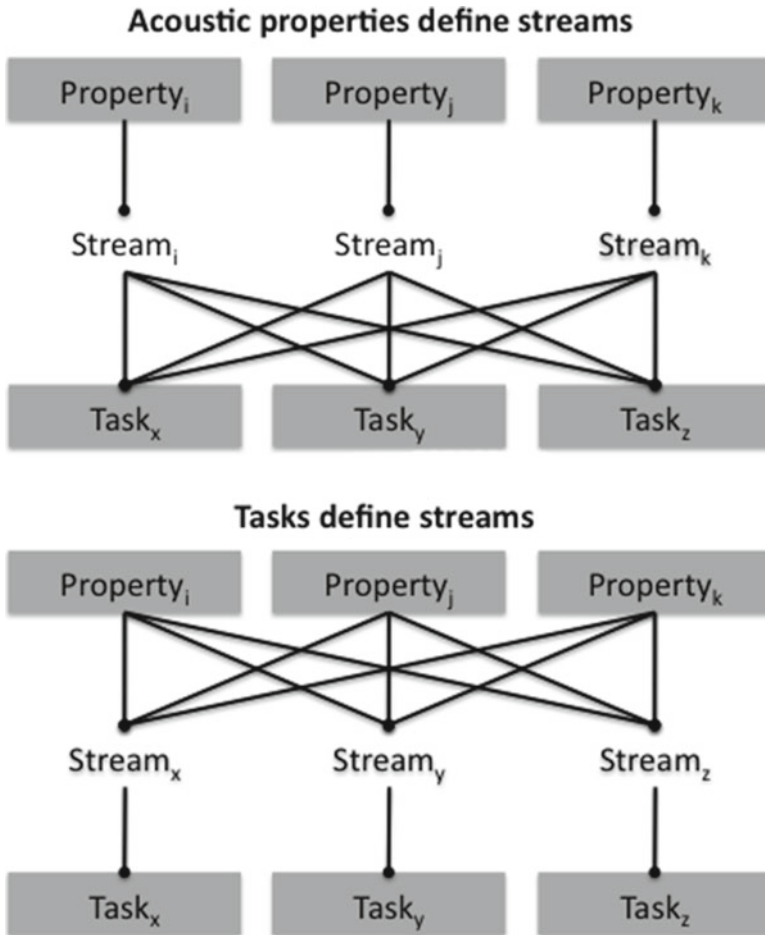
Whereas most research in the auditory system emphasizes stimulus characteristics, for example, spatial versus pitch variation, we suggest that an emphasis on the behavioral goal (task) may be more important in some instances and can clarify issues in the debate over the function of different processing streams in auditory cortex. In theorizing about dorsal and ventral streams within the visual system there has been a shift of focus from stimulus-centered ideas (form vs. space; Ungerleider & Mishkin, 1982) to goal or task-centered ideas (recognition vs. sensory-motor interaction; Milner & Goodale, 1995). This same shift of focus has been emphasized by some authors in the auditory domain (Hickok & Poeppel, 2000, 2007; Warren et al., 2005).

This shift of focus onto the behavioral goals of a task can be generalized to provide a framework for thinking about sensory processing streams. Consider an

example from the spatial domain. A spatially localizable signal has certain sensory features—interaural time difference, interaural level difference, and the particular filtering properties of the outer ear—that can be used to compute location information. However, spatial information can be put to use in a variety of ways. For example, in addition to informing explicit localization decision tasks, spatial information can drive auditory stream segregation (Bregman, 1990) or any number of sensory–motor processes, such as orienting, tracking, approach, or avoidance responses. Note that the goals (effects or output) of these tasks are very different. In auditory stream segregation the goal is to resolve an auditory object, such as a single voice in a noisy room. This is arguably a “ventral stream” function in that the goal is to identify *what* an object is (what is this person saying?). In a sensory–motor process the goal may be to generate a motor command such as a saccade or a head movement or locomotion toward or away from the sound source. And in explicit localization judgments the goal may be to make a spatial decision such as whether one sound occurred in the same or different location than a previous sound. Assuming that different goals (stream segregation, saccade generation, location/motion decision) implicate different neural systems, spatial auditory information must enter into a range of task-dependent, distinct processes. A similar argument could be made for a feature such as frequency (pitch) which could be used for stream segregation, sensory–motor integration (mimicking a tone via humming or reproducing it on a musical instrument), voice identification, explicit pitch discrimination decisions, and so on.

So the same sensory cues can be used for many different task-dependent processes that rely on distinct neural circuits (e.g., sensory–motor vs. sensory recognition vs. frontal decision-related circuits). Information flow within the neural networks supporting these distinct processes can be considered processing “streams.” Therefore, viewed in this way, the streams are task-defined rather than stimulus feature-defined. Figure 12.5 provides a graphic representation of this distinction. The dorsal versus ventral distinction, according to this framework is an oversimplification that reflects a coarse research emphasis on broad categories of processes (e.g., object identification vs. sensory–motor integration) and that ignores any number of potential finer-grained processing streams.

This task-driven framework for understanding processing streams effectively removes “where” from consideration as a viable processing stream because “where” is not a task but a stimulus feature that can be used in the performance of many task goals (Middlebrooks, 2002). This perspective does not preclude the existence of say a cortical “spatial area” that computes spatial location information which then interacts with higher-order networks on a task-dependent basis. In other words, it is logically possible that spatial activations found in the anterior PT correspond to a “feature” processing network in the task-driven model. However, it is also logically possible that the spatial feature processing network is subcortical and the cortical activation found in “spatial” tasks reflects a task-specific network that is putting spatial information to use. This is an empirical question that needs to be addressed explicitly in future work, for example by mapping the distribution of “spatial” responses under a variety of task conditions and identifying those regions that are task-dependent versus task-independent; only the latter would be candidates for “feature processing systems.”



**Fig. 12.5** Schematic depiction of a stimulus- versus a task-based model of sensory processing streams. See text for details

## 12.6 Clinical Evidence and Applications

The PT has been implicated in speech-related symptoms of at least three different disorders, conduction aphasia (noted previously), developmental stuttering, and auditory hallucinations in schizophrenia. The functional relation between the PT and these disorders are discussed in turn.

Developmental stuttering is a disorder affecting speech fluency in which sounds, syllables, or words may be repeated or prolonged during speech production. Auditory input affects fluency in people who stutter. For example, delayed auditory feedback can result in a paradoxical improvement in fluency (Martin & Haroldson, 1979; Stuart et al., 2008). This paradoxical delayed auditory feedback effect is

correlated with planum temporale asymmetry. In one study, stutterers who show the paradoxical delayed auditory feedback effect also had a reversed PT asymmetry (right > left) (Foundas et al., 2004) (recall that PT asymmetry is primarily driven by area Tpt in the posterior PT). And as noted previously, altered auditory feedback modulates activity in the PTR (Fig. 12.3D). Thus, an association exists between the posterior PT, sensory–motor integration, and people who stutter suggesting that Spt (dys)function is involved in this clinical population. It has been suggested that stuttering is caused by dysfunction of internal models involved in motor control of speech, which may result in an over-reliance on sensory feedback that is substantially delayed relative to internal control mechanisms (Max et al., 2004). The work reviewed in this chapter suggests that the posterior PT, area Spt in particular, will be a profitable focus of investigation in this respect.

A prominent positive symptom of schizophrenia is auditory hallucinations, typically involving perceived “voices.” It has (recently) been suggested that this symptom results from imprecise motor-to-sensory corollary discharges (Heinks-Maldonado et al., 2007). Self-generated actions have sensory consequences; for example, moving one’s eyes results in the movement of the visual field across the retina. Yet we do not perceive this sweep across the retina as motion but rather perceive a stable external environment. This is achieved by sending a corollary discharge (forward model) of the motor command to sensory areas, which can be compared against the incoming sensory information to effectively cancel the sensory consequences of self-generated actions. A similar mechanism appears to hold for speech as well, as indicated by the observation that the auditory response to speech is suppressed when speech is self generated (Paus et al., 1996; Heinks-Maldonado et al., 2007). If corollary discharges associated with speech acts (1) are used to distinguish self- from externally generated speech, and (2) if this system is imprecise in schizophrenia, self-generated speech (perhaps even subvocal speech) may be perceived as externally generated, that is, hallucinations. Consistent with this hypothesis, hallucinating patients do not show the normal suppression of auditory response to self-generated speech and the degree of abnormality correlated both with severity of hallucinations and misattributions of self-generated speech (Heinks-Maldonado et al., 2007). Schizophrenics also have anatomical abnormalities of the PT, particularly in the upper cortical layers (I–III, the corticocortical layers) of the caudal PT (~Tpt) in the left hemisphere, which show a reduced fractional volume relative to controls (Smiley et al., 2009). Thus, in schizophrenia the nature of the behavioral and physiological effects (implicating sensory–motor integration,) the location of anatomical abnormalities (left posterior PT), and the level of cortical processing implicated (corticocortical) are all consistent with dysfunction involving area Spt. As with stuttering, a research emphasis on this functional circuit is warranted in understanding aspects of schizophrenia.

One would not have expected a connection between disorders as apparently varied as conduction aphasia, stuttering, and schizophrenia, yet they all seem to involve, in part, dysfunction of the same region and functional circuit. A closer look at these syndromes reveals other similarities. For example, all three conditions show atypical responses to delayed auditory feedback. Fluency of speech in both people who

stutter and conduction aphasics is not negatively affected by delayed auditory feedback and may show paradoxical improvement (Boller et al., 1978; Martin & Haroldson, 1979; Stuart et al., 2008), whereas in schizophrenia delayed auditory feedback induces the reverse effect: greater than normal speech dysfluency (Goldberg et al., 1997). Further, both stuttering and schizophrenia appear to be associated with dopamine abnormalities: dopamine antagonists such as risperidone and olanzapine (atypical antipsychotics commonly used to treat schizophrenia) have recently been shown to reduce stuttering (Maguire et al., 2004). It is unclear how dysfunction of what appears to be the same circuit can result in the range of speech/hearing symptoms found in conduction aphasia, stuttering, and schizophrenia. Rather than a problem, however, having a variety of breakdown scenarios may prove to be particularly instructive in working out the details of the circuit.

## 12.7 Conclusions and Remaining Questions

Neuroanatomical and neurophysiological evidence indicates that the planum temporale is functionally subdivided into (1) an anterior sector that is part of auditory cortex proper and that supports spatial-related but not necessarily spatial-specific functions (such as stream segregation), and (2) a posterior sector that is not part of auditory cortex and which supports sensory–motor integration for vocal tract actions. These functions are likely not restricted to the PT but extend beyond its anatomical boundary to involve cortex extending into the parietal operculum and the superior temporal sulcus. It is also likely that this broader PT region contains further functional subdivisions. For example, the existence of sensory–motor integration processes at both the segmental (individual phonemes) and suprasegmental levels (e.g., pitch and sequences of sounds) was mentioned earlier. There may be distinct, parallel circuits involved in sensory–motor integration at these different levels. Similarly, the cytoarchitectonic subdivisions of the anterior PTR (PaAi, PaAe, PaA c/d) may underlie functional subdivisions between these auditory areas. These issues will require further investigation using within subjects designs and high spatial resolution approaches.

A major functional component of the PTR is sensory–motor integration, particularly for vocal tract actions. Although this circuit has been characterized as the dorsal auditory stream, it seems to be neither purely auditory (Hickok et al., 2009; Okada & Hickok, 2009) nor the only possible dorsal target for auditory information, which also interacts with posterior parietal areas controlling a range of movement systems (Grunewald et al., 1999; Lewis & Van Essen, 2000; Britten, 2008). In light of these observations, we have proposed a refined conceptualization of sensory processing “streams” whereby a stream is defined not by the kinds of computations that are performed within a sensory modality (e.g., pitch vs. location) but by the kinds of task-determined supramodal systems with which a sensory system must interact (e.g., conceptual semantic vs. motor control). On this view, processing streams are not part of a single sensory modality (Pa & Hickok, 2008), rendering terms such as

“auditory dorsal stream” or “visual dorsal stream” outdated at best and misleading at worst. Further, this view moves beyond simple dichotomies, which increasingly fall short in explaining the range of empirical observations (Rossetti et al., 2003; Pisella et al., 2009), and affords the possibility that the same sensory information (e.g., location) can enter into multiple higher-order processing streams depending on how that information is put to use.

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