

ventral pathway is responsible for identifying the speaker. Similarly, the dorsal pathway processes the melody of an instrumental piece, while the ventral pathway recognizes the instrument by its timbre. This 'What/How' model of functional segregation requires experimental confirmation. In particular, it will be important to understand how such functional segregation interacts with hemispheric lateralization, a feature of the auditory cortex that characterizes the human brain.

Pascal Belin and Robert J. Zatorre  
*Neuropsychology/Cognitive Neuroscience Unit,  
Montreal Neurological Institute, McGill  
University, Montréal, Québec, Canada  
email (P.B.): pascal@bic.mni.mcgill.ca*

REPLY—Belin and Zatorre suggest that the anatomical segregation noted in our analysis of auditory-prefrontal connections<sup>1</sup> might reflect 'What' and 'How' rather than 'What' and 'Where' streams of auditory information processing. They state that there is "little evidence for circumscribed areas of the auditory cortex being uniquely specialized for processing auditory spatial information...." Furthermore, Belin and Zatorre propose that, as applied to speech perception, their model supports a dorsal pathway for extracting a verbal message and a ventral pathway for identifying the speaker.

In response, we point to several lines of evidence linking posterior auditory belt cortex and dorsolateral prefrontal cortex with auditory spatial processing. A number of studies have shown that neurons within the posterior auditory cortex are activated during sound location perception<sup>11,12</sup>. Recanzone and colleagues<sup>13</sup> recently found that more neurons in caudal areas had spatial sensitivity consistent with behavioral responses when compared to A1 neurons. No topographic spatial 'maps' have as yet been found in any of these studies. However, such maps are by no means a necessity, because cortex (unlike the colliculi) may not use a place code for the representation of auditory space. Similarly, the use of population codes<sup>7</sup> and spike timing<sup>14</sup> is not at all mutually exclusive with the existence of a 'where' pathway. In addition to nonhuman primate work, human imaging studies have also demonstrated posterior cortical activation during the spatial perception of sound<sup>15</sup>. Furthermore, abnormal sound localization has been observed in patients with lesions of posterior auditory cortex<sup>16</sup>.

In the frontal lobe, the caudal dorso-lateral region (areas 8 and 46) is involved

in visuo-spatial perception and memory in non-human primates as well as humans<sup>17</sup>, and this same region receives a selective innervation from the caudal auditory belt<sup>1</sup>. Moreover, recordings from non-human primates have shown that the responses of some neurons in dorsolateral prefrontal cortex are dependent upon sound source location<sup>18</sup>. Furthermore, the same regions (together with posterior parietal cortex) are active during sound localization in man<sup>19</sup>. Therefore, based on anatomical projections, electrophysiology and functional imaging there is evidence supporting a dorsal auditory spatial pathway.

An important point raised by Belin and Zatorre is how the human posterior auditory cortex might figure into a dorsal 'where' pathway, because it is obviously also involved in speech perception. We concur that 'motion processing' in a general sense may indeed be one of the functions of the dorsal pathway but suggest that it can be used in the service of both auditory space processing and speech perception. As Belin and Zatorre point out, auditory 'motion' can be understood both by functional analogy with the visual system as real 'motion in space' or by direct sensory analogy as 'spectral motion' of a frequency modulation across the sensory epithelium<sup>20</sup>. Frequency sweeps in the latter sense are ubiquitous components of communication sounds, including human speech where they figure prominently as formant transitions. Neurons in both the rostral and caudal auditory belt are selective for the direction and speed of spectral motion<sup>20</sup>, which underscores their potential role in the pre-processing of speech. Only neurons in the caudal belt, however, are highly selective for spatial position as well (J.P.R. *et al.*, *Soc. Neurosci. Abstr.* 25, 157.2, 1999). It seems, therefore, that the caudal belt may combine both the spectral and spatial elements of auditory motion processing and may act as a switchboard at which a 'where' pathway originates and further processing of speech takes place. As Kaas and Hackett<sup>2</sup> explain in their *News & Views* comments on our original paper<sup>1</sup>, the number of auditory processing streams is by no means limited to two, but may consist of several 'streamlets' involved in various aspects of auditory perception. Like Belin and Zatorre's model, our model too requires experimental confirmation, and perhaps exchanges, such as this, will encourage those research efforts.

Lizabeth M. Romanski<sup>1</sup>, Biao Tian<sup>2</sup>,  
Jonathan B. Fritz<sup>3</sup>,  
Mortimer Mishkin<sup>3</sup>,  
Patricia S. Goldman-Rakic<sup>4</sup> and  
Josef P. Rauschecker<sup>2</sup>

<sup>1</sup> Dept. Neurobiology & Anatomy, University of Rochester, 601 Elmwood Ave., Box 603, Rochester, New York 14642, USA

<sup>2</sup> Georgetown Institute for Cognitive and Computational Science, Georgetown University Medical Center, New Research Bldg., Rm. WP15, 3970 Reservoir Road NW, Washington, DC 20007-2197, USA

<sup>3</sup> Laboratory of Neuropsychology, NIMH, Building 49, Room 1B80, Bethesda, Maryland 20892-4415, USA

<sup>4</sup> Section of Neurobiology, Yale University School of Medicine, New Haven, Connecticut, USA  
email (J.P.R.): rauschecker@giccs.georgetown.edu

- Romanski, L. M. *et al.* *Nat. Neurosci.* 2, 1131–1136 (1999).
- Kaas, J. H. & Hackett, T. A. *Nat. Neurosci.* 2, 1045–1047 (1999).
- Rauschecker, J. P. *Curr. Opin. Neurobiol.* 8, 516–521 (1998).
- Belin, P., Zatorre, R. J., Lafaille, P., Ahad, P. & Pike, B. *Nature* 403, 309–312 (2000).
- Cohen, Y. E. & Wessinger, C. M. Who goes there? *Neuron* 24, 769–771 (1999).
- Brainard, M. S. Neural substrates of sound localization. *Curr. Opin. Neurobiol.* 4, 557–562 (1994).
- Fitzpatrick, D. C., Batra, R., Stanford, T. R. & Kuwada, S. *Nature* 388, 871–874 (1998).
- Wernicke, C. *Der aphasische Symptomencomplex* (Cohn & Weigert, Breslau, 1874).
- Zatorre, R. J., Evans, A. C., Meyer, E. & Gjedde, A. *Science* 256, 846–849 (1992).
- Thivard, L., Belin, P., Zilbovicius, M., Poline, J. B. & Samson, Y. *Neuroreport* (in press).
- Leinonen, L., Hyvärinen, J. & Sovijärvi, A. R. *Exp. Brain Res.* 39, 203–215 (1980).
- Rauschecker, J. P., Tian, B., Pons, T. & Mishkin, M. *J. Comp. Neurol.* 382, 89–103 (1997).
- Recanzone, G. H., Guard, D. C., Phan, M. L. & Su, T. K. *J. Neurophysiol.* 83, 2723–2739 (2000).
- Middlebrooks, J. C., Clock, A. E., Xu L. & Green D. M. *Science* 264, 842–844 (1994).
- Griffiths, T. D. *et al.* *Nat. Neurosci.* 1, 74–79 (1998).
- Clarke, S., Bellmann, A., Meuli, R. A., Assal, G. & Steck, A. J. *Neuropsychologia* 38, 797–807 (2000).
- Goldman-Rakic, P. S. *Phil. Trans. Roy. Soc. Lond. B: Biol. Sci.* 351, 1445–1453 (1996).
- Vaadia, E., Benson, D. A., Hienz, R. D. & Goldstein, M. H., Jr. *J. Neurophysiol.* 56, 934–952 (1986).
- Bushara, K., *et al.* *Nat. Neurosci.* 2, 759–766 (1999).
- Rauschecker, J. P. *Audiol. Neurootol.* 3, 86–103 (1998).