

Neural Mechanisms Underlying Melodic Perception and Memory for Pitch

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The neural correlates of music perception were studied by measuring cerebral blood flow (CBF) changes with positron emission tomography (PET). Twelve volunteers were scanned using the bolus water method under four separate conditions: (1) listening to a sequence of noise bursts, (2) listening to unfamiliar tonal melodies, (3) comparing the pitch of the first two notes of the same set of melodies, and (4) comparing the pitch of the first and last notes of the melodies. The latter two conditions were designed to investigate short-term pitch retention under low or high memory load, respectively. Subtraction of the obtained PET images, superimposed on matched MRI scans, provides anatomical localization of CBF changes associated with specific cognitive functions. Listening to melodies, relative to acoustically matched noise sequences, resulted in CBF increases in the right superior temporal and right occipital cortices. Pitch judgments of the first two notes of each melody, relative to passive listening to the same stimuli, resulted in right frontal-lobe activation. Analysis of the high memory load condition relative to passive listening revealed the participation of a number of cortical and subcortical regions, notably in the right frontal and right temporal lobes, as well as in parietal and insular cortex. Both pitch judgment conditions also revealed CBF decreases within the left primary auditory cortex. We conclude that specialized neural systems in the right superior temporal cortex participate in perceptual analysis of melodies; pitch comparisons are effected via a neural network that includes right prefrontal cortex, but active retention of pitch involves the interaction of right temporal and frontal cortices.

[Key words: human auditory processing, music, pitch, auditory working memory, PET, temporal cortex, frontal cortex]

Perceiving a melody, or sequence of pitches, requires relatively complex perceptual analysis, since short-term memory and abstract pattern-matching mechanisms must be involved (Deutsch, 1982; Dowling and Harwood, 1986). It seems likely that such processing would also demand a correspondingly complex set

of neural computations, but at present, the cerebral substrates for melodic processing remain poorly understood. Current knowledge of complex auditory neural processing comes from two principal sources: neuroanatomical and neurophysiological studies of the auditory system of nonhuman vertebrates, and studies of the effects of human brain lesions on auditory tasks. Each of these will be briefly reviewed before introducing the present investigation, which takes advantage of recent advances in PET brain imaging techniques to study the functional cerebral systems involved in melodic perception in the living human brain.

The superior aspect of the temporal lobe has long been known to contain neurons responsive to auditory stimulation in both monkey (Ferrier, 1876; Merzenich and Brugge, 1973) and human (Flechsig, 1896; Celestia, 1976). Several distinct cortical fields may be identified on the basis of the neurophysiological response properties of neurons within those fields (Brugge and Reale, 1985), and also based on their cytoarchitectonic characteristics. A general distinction may be drawn between the primary auditory area—or toniocortex—lying deep within Heschl's gyri in the human brain (Galaburda and Sanides, 1980; Liegeois-Chauvel et al., 1991), and surrounding regions, which may be termed secondary or associative auditory cortex. Some of these cortical fields are arranged tonotopically (Woolsey, 1971; see Brugge and Reale, 1985, for a review), suggesting that they play a role in frequency analysis. However, apart from the primary and immediately surrounding regions, the frequency tuning of individual units can be very broad, and the tonotopic organization can be difficult to discern (Manley and Müller-Preuss, 1978). Some neurons respond best to complex stimuli, such as tones modulated in frequency (Whitfield and Evans, 1965), or patterns of ascending or descending tone sequences (McKenna et al., 1989).

The morphological and physiological distinctions between cortical regions raise important questions regarding the consequences of such an architecture for auditory processing. Can dissociations be identified that would allow functional significance to be assigned to the structural heterogeneity? A possible functional role for human superior temporal neurons in higher-order auditory processes is suggested by the observations of Penfield and Perot (1963) and of Penfield and Jasper (1954). They noted that complex auditory sensations (including voices and music) could be elicited from electrical stimulation of the exposed cortex in this region, but not from Heschl's gyri, which instead usually resulted in more elementary sensations, such as buzzing.

The connectivity of these regions indicates that both primary and secondary areas receive input from various divisions of the medial geniculate nucleus (Burton and Jones, 1976), suggesting

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Melodic Perception

Clifford Lane



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