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The Cortical Topography of Tonal Structures Underlying Western Music

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Western tonal music relies on a formal geometric structure that determines distance relationships within a harmonic or tonal space. In functional magnetic resonance imaging experiments, we identified an area in the rostromedial prefrontal cortex that tracks activation in tonal space. Different voxels in this area exhibited selectivity for different keys. Within the same set of consistently activated voxels, the topography of tonality selectivity rearranged itself across scanning sessions. The tonality structure was thus maintained as a dynamic topography in cortical areas known to be at a nexus of cognitive, affective, and mnemonic processing.

The use of tonal music as a stimulus for probing the cognitive machinery of the human brain has an allure that derives, in part, from the geometric properties of the theoretical and cognitive structures involved in specifying the distance relationships among individual pitches, pitch classes (chroma), pitch combinations (chords), and keys (*1–3*). These distance relationships shape our perceptions of music and allow us, for example, to notice when a pianist strikes a wrong note. One geometric property of Western tonal music is that the distances among major and minor keys can be represented as a tonality surface that projects onto the doughnut shape of a torus (*1, 4*). A piece of music elicits activity on the tonality surface, and harmonic motion can be conceptualized as displacements of the activation focus on the tonality surface (*3*). The distances on the surface also help govern expectations that actively arise while

one listens to music. Patterns of expectation elicitation and fulfillment may underlie our affective responses to music (*5*).

Two lines of evidence indicate that the tonality surface is represented in the human brain. First, when one subjectively rates how well each of 12 probe tones, drawn from the chromatic scale (*6*), fits into a preceding tonal context that is established by a single chord, chord progression, or melody, the rating depends on the relationship of each tone to the instantiated tonal context. Nondiatonic tones that do not occur in the key are rated as fitting poorly, whereas tones that form part of the tonic triad (the defining chord of the key) are judged as fitting best (*2*). Probe-tone profiles obtained in this manner for each key can then be correlated with the probe-tone profile of every other key to obtain a matrix of distances among the 24 major and minor keys. The distance relationships among the keys readily map onto the surface of the torus (*4*). Thus, there is a direct correspondence between music-theoretic and cognitive descriptions of the harmonic organization of tonal music (*7*).

Second, electroencephalographic studies of musical expectancy (*8–11*) have examined the effect of melodic and harmonic

context violations on one or more components of event-related brain responses that index the presence and magnitude of context violations. Overall, the cognitive distance of the probe event from the established harmonic context correlates positively with the amplitudes of such components. These effects appear even in listeners without any musical training (*9, 11*). The perceptual and cognitive structures that facilitate listening to music may thus be learned implicitly (*2, 12–15*).

The prefrontal cortex has been implicated in the manipulation and evaluation of tonal information (*10, 11, 16–18*). However, the regions that track motion on the tonality surface have not been identified directly. When presented with a stimulus that systematically moves across the entire tonality surface, will some populations of neurons respond selectively to one region of the surface and other populations respond selectively to another region of the surface?

Identification of tonality-tracking brain areas. In order to identify cortical sites that were consistently sensitive to activation changes on the tonality surface, eight musically experienced listeners (see "subjects" in supporting online text) underwent three scanning sessions each, separated by 1 week on average, in which they performed two perceptual tasks during separate runs. During each run, they heard a melody that systematically modulated through all 12 major and 12 minor keys (see "stimuli and tasks" in supporting online text) (Fig. 1 and audio S1). A timbre deviance detection task required listeners to respond whenever they heard a note played by a flute instead of the standard clarinet timbre, whereas a tonality violation detection task required listeners to respond whenever they perceived notes that violated the local tonality (Fig. 1D). The use of two tasks that required attentive listening to the same melody but different perceptual analyses facilitated our primary goal of identifying cortical areas that exhibit tonality tracking that is largely independent of the specific task that is being performed (see "scanning procedures" in supporting online

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Fig. 1. Properties of the tonality surface and behavioral response profiles. In the key names, capital letters indicate major keys and lowercase letters indicate minor keys. (**A**) Unfolded tori showing the average tonality surfaces for each of the 24 keys in the original melody. The top and bottom edges of each rectangle wrap around to each other, as do the left and right edges. θ and φ refer to the angular position along each of the circles comprising the torus. The color scale is arbitrary, with red and blue indicating strongest and weakest activation, respectively. Starting with C major and shifting from left to right, the activation peak in each panel reflects the melody's progression through all of the keys. (**B**) The circle of fifths. Major keys are represented by the outside ring of letters. Neighboring keys have all but one of their notes in common. The inner ring depicts the (relative) minor keys that share the same key signature (number of sharps and flats) with the adjacent major key. The color code refers to the three groups of keys into which tonality tracking voxels were categorized (Fig. 3). (**C**) Correlations among the average tonality surface topographies for each key. The topographies of keys that are closely related in a music-theoretic sense are also highly positively correlated, whereas those that are distantly related are negatively correlated. Three groups of related keys, indicated in (B), were identified by singular value decomposition of this correlation matrix. (**D**). Average response profiles (eight listeners, three sessions each) from the tonality deviance detection task illustrate the propensity of specific test tones to pop out and elicit a response in some keys but not in others over the course of the melody. Error bars reflect 1 SEM.
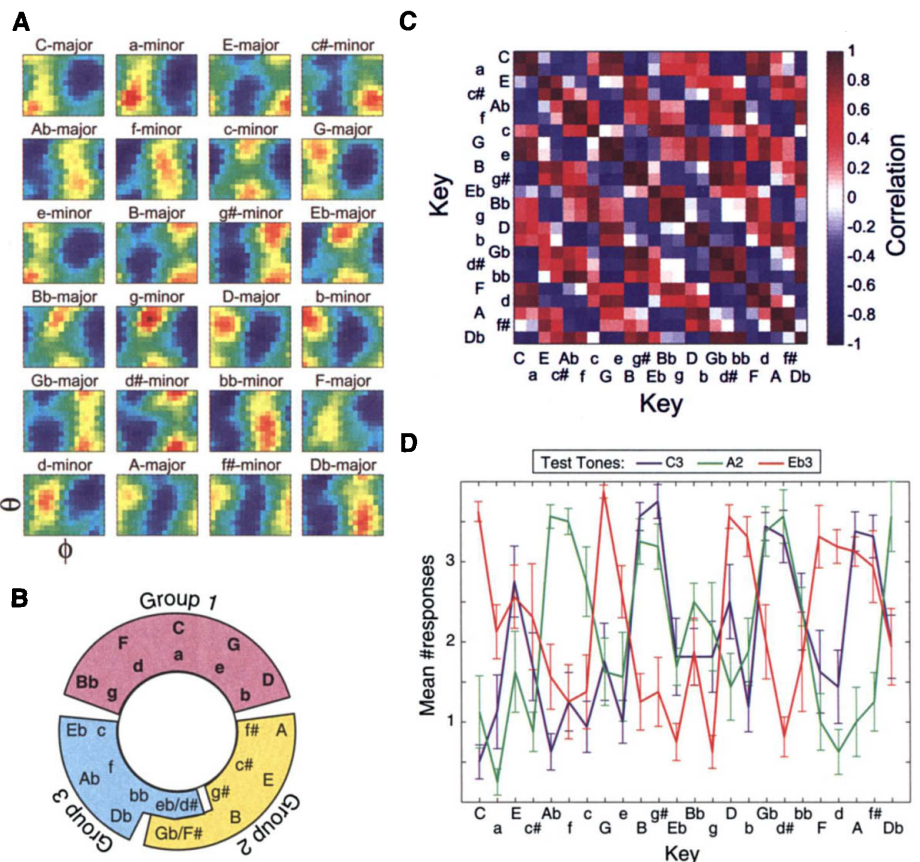

text). Using a regression analysis with separate sets of regressors to distinguish task effects from tonality surface tracking, we identified task- and tonality-sensitive areas (see "fMRI analysis procedures" in supporting online text). Tonality regressors were constructed from the output of a neural network model of the moment-to-moment activation changes on the tonality surface (see "tonality surface estimation" in supporting online text).

Our tasks consistently activated several regions in the temporal, parietal, frontal, and limbic lobes as well as the thalamus and cerebellum. The most extensive consistent activation was along the superior temporal gyrus (STG) of both hemispheres, though the extent was greater in the right hemisphere, stretching from the planum temporale to the rostral STG and middle temporal gyrus (Fig. 2A and Table 1). Both the task and the tonality regressors correlated significantly and consistently with activity in the rostromedial prefrontal cortex, primarily in the rostral and ventral reaches of the superior frontal gyrus (SFG) (Figs. 2 and 3). The consistent modulation of this area in all of our listeners led us to focus on this region as a possible site of a tonality map.

Tonality-specific responses in the rostromedial prefrontal cortex. At the

Fig. 2. Group conjunction maps showing the consistency with which specific structures were activated across listeners. Conjunction maps of individual listeners, containing the voxels that were activated significantly ($P < 0.001$) in all scanning sessions for that listener, were normalized into a common space and summed together across listeners (see "spatial normalization" in supporting online text). Voxels that were consistently activated by at least four of the eight listeners are projected onto the group's mean normalized T1 image. (**A**) Areas sensitive to the two task regressors (Table 1). (**B**) The only areas whose activity patterns were significantly and consistently correlated with the tonality regressors both within and across listeners were the rostral portion of the ventromedial superior frontal gyrus and the right orbitofrontal gyrus.
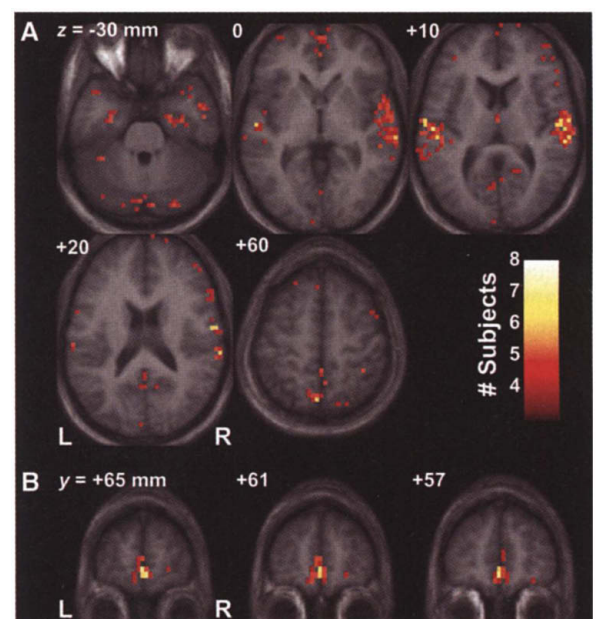
individual level, we reconstructed and categorized the tonality sensitivity surface (TSS) for each voxel that exhibited significant responses ($P < 0.001$) in every one of the three scanning sessions (see "tonality surface estimation" in supporting online text). The

reconstructed surfaces from each session indicated that the medial prefrontal cortex maintains a distributed topographic representation of the overall tonality surface (Fig. 3). Although some voxels exhibited similar TSSs from session to session, the global tonality
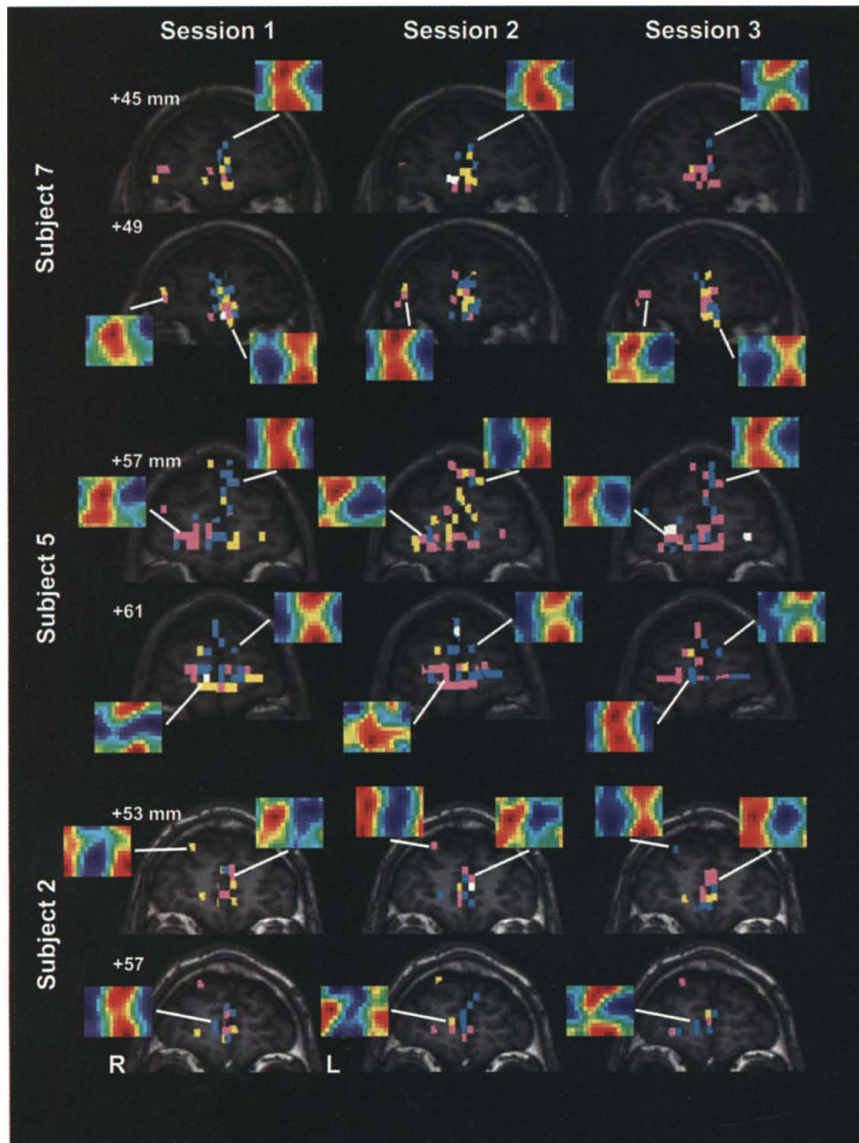
Fig. 3. Topography of tonality sensitivity of rostroventral prefrontal cortex in three listeners across three scanning sessions each. Each voxel's color represents the key group with which the voxel's TSS was maximally correlated (Fig. 1B). The minority of voxels that were maximally correlated with the average tonality surface are shown in white. A TSS represents how sensitive the voxel is to each point on the torus. The TSSs of selected voxels are displayed as unfolded tori. Figure 1A serves as a legend for assigning keys to the individual TSSs. The highlighted voxels were chosen to display both the consistency and heterogeneity of the tonality surfaces across sessions. For each listener, the activity of all voxels shown was significantly correlated with the tonality regressors in all sessions. Thus, what changed between sessions was not the tonality-tracking behavior of these brain areas but rather the region of tonal space (keys) to which they were sensitive. This type of relative representation provides a mechanism by which pieces of music can be transposed from key to key, yet maintain their internal pitch relationships and tonal coherence.

topography varied across sessions in each of the listeners. The number of voxels falling into each of the tonality categories (Fig. 1B) was evenly distributed within each session (table S1), but the relative pattern of tonality sensitivity changed. For all listeners, we also found tonality-sensitive voxels outside of the medial prefrontal region (table S2). The precise constellations of sensitive areas differed across listeners. We found tonality-sensitive foci in the orbital and frontal gyri, primarily

in the right hemisphere; the temporal pole; the anterior and posterior superior temporal sulci; the precuneus and superior parietal gyrus; the posterior lingual gyrus; and the cerebellum (19).

Discussion. Central to our ability to hear music coherently are cognitive structures that maintain perceptual distance relationships among individual pitches and groups of pitches. These structures shape expectations about pitches we will hear,

given a preceding musical input. Given the diversity of the music we hear, the situations in which we hear it, and our affective and motoric responses to it, it is likely that tonal contexts are maintained in cortical regions predisposed to mediating interactions between sensory, cognitive, and affective information. The medial prefrontal cortex is a nexus for such functions (20, 21) and is therefore an ideal region for maintaining a tonality map. In the macaque, connections to the medial prefrontal cortex from unimodal sensory cortices are widespread for the auditory modality and sparse for the other sensory modalities (22). In our experiments, we observed significant task-related activity in auditory association areas and the anterior STG, primarily in the right hemisphere. Reciprocal projections between these areas and the ventral medial prefrontal cortex help explain how and why a tonality map might be maintained in the medial prefrontal cortex. This region has already been implicated in assessing the degree of musical consonance or dissonance caused by a harmonic accompaniment to a melody (23). Our results suggest that the rostromedial prefrontal cortex not only responds to the general degree of consonance but actively maintains a distributed topographic representation of the tonality surface. The perception of consonance and dissonance depends on intact auditory cortices (24, 25). However, even with bilateral auditory cortex ablations, the ability to generate expectancies based on tonal contexts remains, suggesting that the cognitive structures maintaining tonal knowledge largely reside outside of temporal lobe auditory structures (24).

Dynamic topographies. In contrast to distributed cortical representations of classes of complex visual objects that appear to be topographically invariant (26), we found that the mapping of specific keys to specific neural populations in the rostromedial prefrontal cortex is relative rather than absolute. Within a reliably recruited network, the populations of neurons that represent different regions of the tonality surface are dynamically allocated from one occasion to the next. This type of dynamic topography may be explained by the properties of tonality structures. In contrast to categories of common visual objects that differ in their spatial features, musical keys are abstract constructs that share core properties. The internal relationships among the pitches defining a key are the same in each key, thereby facilitating the transposition of musical themes from one key to another. However, the keys themselves are distributed on a torus at unique distances from one another. A dynamic topography may also arise from the interplay of short-term and long-term memory stores of tonal information and may serve

Table 1. Loci consistently showing a main effect of task in a majority of listeners. MTG, middle temporal gyrus; IFG, inferior frontal gyrus; SPG, superior parietal gyrus.

Lobe	Region (Brodmann area)	Left hemisphere					Right hemisphere				
		Location (mm)			Listeners at peak (no.)	Cluster size (voxels)	Location (mm)			Listeners at peak (no.)	Cluster size (voxels)
		x	y	z			x	y	z		
Temporal											
	STG (22)	-64	-11	10	6	74					
	STG/Heschl's gyrus (41/42)	-56	-19	9	7	74	52	-11	5	8	163
	STG/planum temporale (22)	-68	-41	15	5	14	64	-30	15	6	163
							64	-26	5	6	163
	Rostromedial STG						38	15	-35	5	36
	Rostroventral MTG (21)						52	0	-35	6	36
	Middle MTG/superior temporal sulcus (21)						56	-15	-15	5	163
	Ventral MTG (21)						60	-11	-25	6	163
Frontal											
	Rostroventromedial SFG (10/14)	0	49	0	5	27	4	64	0	5	27
	Superior frontal sulcus/frontopolar gyrus (10)						26	64	30	5	3
	Lateral orbital gyrus (11)						49	41	-10	5	4
	IFG, pars orbitalis (47)						49	45	4	5	3
	IFG, pars opercularis (44)						56	19	5	6	3
							60	22	20	4	11
	Precentral gyrus (6)						49	4	55	5	10
Parietal											
	Postcentral gyrus (1)						64	-11	25	6	163
	Supramarginal gyrus (40)						64	-30	35	6	3
	Precuneus (7)	0	-45	55	5	42	0	-45	55	5	42
		-4	-56	75	6	42					
	SPG (7)						11	-56	80	5	3
							19	-49	75	6	5
	SPG/transverse parietal sulcus (7)	-4	-71	60	6	22					
Limbic											
	Collateral sulcus	-30	-8	-30	5	10					
	Hippocampus/collateral sulcus						26	-11	-25	5	23
Other											
	Cerebellum	-4	-82	-35	5	11					
		-38	-79	-25	6	19	26	-86	-30	5	10
							45	-64	-45	5	8
	Mediodorsal thalamic nucleus	0	-11	9	5	3					

a beneficial role in coupling the moment-to-moment perception of tonal space with cognitive, affective, and motoric associations, which themselves may impose constraints on the activity patterns within rostral prefrontal regions (*21, 27–29*).

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6. The chromatic scale consists of 12 equally sized intervals into which an octave is divided. On a piano, a chromatic scale starting at middle C would be played by striking adjacent keys until the note C, either one octave above or below middle C, was reached.
7. The extent to which tonality representations are maintained in long-term or short-term memory stores, or a combination of the two, is a matter of debate. Self-organizing neural network models of implicit learning accurately mimic results from a wide array of experiments that assess tonal knowledge (*15*), and harmonic priming experiments directly highlight the influence of learned tonal structures (*13, 30*). However, models of short-term sensory memory account for significant proportions of the variance in probe-tone experiments (*31, 32*), and

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