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Functional anatomy of musical processing in listeners with absolute pitch and relative pitch

ROBERT J. ZATORRE*†, DAVID W. PERRY*, CHRISTINE A. BECKETT‡, CHRISTOPHER F. WESTBURY*, AND ALAN C. EVANS*

*Montreal Neurological Institute, and ‡Faculty of Music, McGill University, Montreal, Quebec, Canada H3A 2B4

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ABSTRACT **We used both structural and functional brain imaging techniques to investigate the neural basis of absolute pitch (AP), a specialized skill present in some musicians. By using positron emission tomography, we measured cerebral blood flow during the presentation of musical tones to AP possessors and to control musicians without AP. Listening to musical tones resulted in similar patterns of increased cerebral blood flow in auditory cortical areas in both groups, as expected. The AP group also demonstrated activation of the left posterior dorsolateral frontal cortex, an area thought to be related to learning conditional associations. However, a similar pattern of left dorsolateral frontal activity was also observed in non-AP subjects when they made relative pitch judgments of intervals, such as minor or major. Conversely, activity within the right inferior frontal cortex was observed in control but not in AP subjects during the interval-judgment task, suggesting that AP possessors need not access working memory mechanisms in this task. MRI measures of cortical volume indicated a larger left planum temporale in the AP group, which correlated with performance on an pitch-naming task. Our findings suggest that AP may not be associated with a unique pattern of cerebral activity but rather may depend on the recruitment of a specialized network involved in the retrieval and manipulation of verbal–tonal associations.**

The existence of special perceptuomotor skills in certain individuals presents many puzzling questions for cognitive neuroscience. One such ability whose cerebral substrate remains essentially unknown is absolute pitch (AP), also known as perfect pitch, a relatively rare ability that refers to a long-term internal representation for the pitch of tones in the musical scale (1, 2). It is typically manifested behaviorally by the ability to identify, by the name of the musical note, the pitch of any sound without reference to another sound or by producing a given musical tone on demand. In contrast, relative pitch (RP), which is well-developed among most trained musicians, refers to the ability to make pitch judgments about the relation between notes, such as within a musical interval.

Knowledge about the neural basis for AP is sparse, but three pieces of information are relevant. (*i*) A case study (3) of an AP possessor who underwent surgical excision within the left temporal lobe for control of epilepsy did not find any deterioration of AP ability; instead, some improvement was noted, which was attributed to a reduction of interference from seizure activity. This finding would suggest that AP does not depend on the integrity of the left anterior temporal lobe but does not clarify which neural structures are crucial for the expression of AP. (*ii*) Anatomical structural measurements (4) have indicated that there is a more marked left hemispheric asymmetry among AP subjects in the region of the planum temporale (PT), an area of associative auditory cortex often thought to be related to language processes (5). Although this finding suggests that the PT may play some role in the AP phenomenon, its functional significance remains to be clarified. (*iii*) Finally, a number of electrophysiological studies have also been carried out (6–8) that indicate a reduction or absence of the P300-evoked response in AP subjects. This finding remains open to interpretation, but one possibility is that it may reflect a lack of updating in auditory working memory among AP possessors.

Recent developments in brain imaging now permit both functional and structural measures to be obtained *in vivo*. Positron emission tomography (PET), in particular, has been used to elucidate the neural activity associated with a number of cognitive functions, including pitch processing and music (9–11). Given the uncertainty surrounding the neural mechanisms that may underlie AP, and the difficulty in integrating the few findings that are in the literature, we chose to use PET to measure cerebral blood flow (CBF) activation among AP subjects and to perform anatomical measurements of the PT with MRI. The study had four specific aims: (*i*) to test whether specific cerebral regions are differentially active in AP musicians when listening to and making judgments about tonal stimuli, and if so to identify them; (*ii*) to test whether functional differences between AP and control subjects disappear during the performance of a RP task that does not require AP; (*iii*) to determine whether the reported structural asymmetry in the PT (4) could be replicated and to observe whether it bears any relation to functional measures; and (*iv*) to test the hypothesis (6–8) that working memory mechanisms for pitch are different for AP listeners as compared with musicians without this ability.

METHODS

Subjects. Twenty right-handed musically trained volunteers (Table 1) were included in the study. All subjects underwent a screening procedure, which required them to identify by musical note name a series of 100 synthetic tones (identical to those used in the PET study) randomly selected from an equal-tempered scale. Ten self-identified AP possessors whose average error scores were within 0.6 semits (1 semit equals 1/12 of an octave in equal logarithmic steps) of the target were retained (see Table 1); two others were rejected. Ten other musicians whose reports of good RP but no AP were confirmed by screening were assigned to the RP group. All subjects gave informed consent for participation, in accordance with ethical guidelines in place at our institution.

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Abbreviations: AP, absolute pitch; RP, relative pitch; PET, positron emission tomography; CBF, cerebral blood flow; PT, planum temporale; DLF dorsolateral frontal.

†To whom reprint requests should be addressed at: Montreal Neurological Institute, 3801 University Street, Montreal, Quebec, Canada H3A 2B4. e-mail: md37@musica.mcgill.ca.

Table 1. Subject characteristics, performance on screening test, performance on minor/major task, and mean volume PT

Group	Age, years	Musical experience, years	Screening mean error, semits	Minor/Major task		PT volume, mm^3	
				% corr	Latency, msec	Left	Right
AP	24.5	18.2	0.16	96.7	2224	4950	4557
	(4.1)	(6.3)	(0.2)	(4.5)	(232)	(811)	(1259)
RP	24.8	13.1	2.44	82.8	2335	4160	4029
	(6.6)	(6.9)	(1.0)	(13.5)	(275)	(1045)	(897)

Numbers in parentheses are the SD. corr, Correct.

Stimuli. Two types of stimuli were created, noise bursts and tones. Tones were synthesized by using the first 15 harmonics of a sawtooth waveform; the fundamental frequencies selected spanned the range from F#3 (185 Hz) to C#5 (554.4 Hz). Each tone was 500 msec in duration, with a 50-msec quarter sine wave rise time, a 300-msec steady-state portion, and a 150-msec exponential decay (Fig. 1*A*). Noise stimuli were synthesized by passing white noise through the identical temporal envelope used for the tones (see Fig. 1*B*), resulting in stimuli with similar duration and onset/offset characteristics. During testing, tones were presented in pairs that formed a musical interval (Fig. 1*C*). The two stimuli within a pair were presented without pause; the intertrial interval was 1,800 msec. For each condition a continuous sequence of randomly selected stimulus pairs was presented throughout the entire scan interval. Overall amplitudes of tones and noise stimuli were equalized via a sound-pressure meter. Stimuli were presented binaurally at a level of about 75 dB sound pressure level (A) via Eartone type 3A insert earphones.

Procedure. Three PET scans were obtained: one baseline and two active conditions. In the noise condition, which served as a baseline, subjects heard pairs of noise bursts acoustically matched to the tones they would hear in the other two conditions (Fig. 1*A*) and pressed a key after each pair. This baseline thus serves as a sensory/motor control condition. In the two activation conditions subjects were presented with pairs of sequential tones that formed musical intervals (Fig. 1*C*), either descending or ascending minor or major thirds. In the tones condition, they were simply instructed to listen to these tones and to press a key after each pair. In the minor/major condition subjects heard stimuli identical to those heard in the tones condition, but this time were instructed to determine the interval formed (a judgment that may be accomplished via RP) and to make an appropriate key press. Order of stimuli within the two active conditions was randomized. Latency (from stimulus onset) and accuracy data were collected on-line during scanning. Subjects maintained their eyes closed at all times during performance of the tasks.

Imaging and Analysis. PET scans were obtained with a Scanditronix PC-2048B 15-slice tomograph. The distribution of CBF was measured during each 60-sec scan using the O-15 water bolus method (12). MRI scans (160 1-mm-thick slices) were also obtained for each subject with a 1.5-T Phillips Gyroscan ACS to provide anatomical detail and for morphometric analysis (see below). CBF images were reconstructed by using an 18-mm Hanning filter, normalized for differences in global CBF, coregistered with the individual MRI data (13), and transformed into the standardized Talairach stereotaxic space (14) via an automated feature-matching algorithm (15). PET images were averaged across subjects for each condition

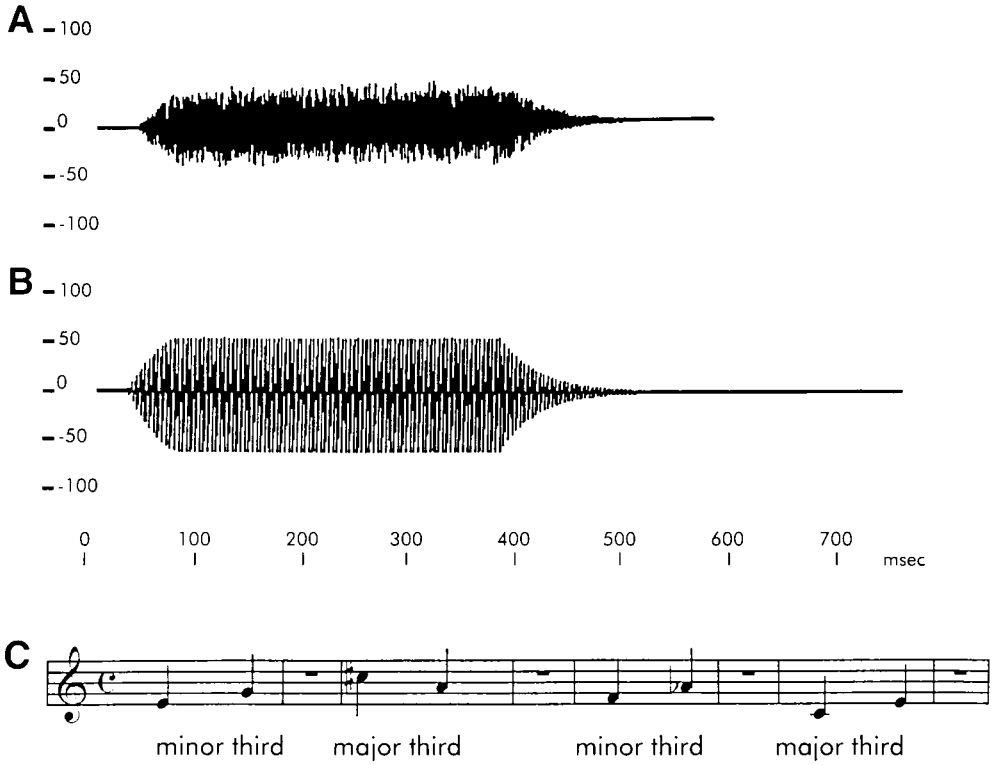

FIG. 1. (*A*) Waveforms of stimuli used for the noise (baseline) condition. (*B*) Waveforms for tones used in the activation conditions; note similar amplitude envelope and duration across stimuli. (*C*) Example of stimulus sequence used, in musical notation, for tones and minor/major conditions.

and the mean change image volume obtained for each comparison; this volume was converted to a *t* statistic map, and the significance of focal CBF changes was assessed by a method based on three-dimensional Gaussian random-field theory (16). The threshold for significance was set at $t = 3.5$ ($P < 0.0004$, uncorrected), resulting in an average of 0.58 false positive per search volume of 200 resolution elements (of dimension $18 \times 18 \times 7.6$ mm), which corresponds approximately to the volume of gray matter scanned. Weaker foci ($2.9 < t < 3.5$) are also reported in the case of closely corresponding (<20 mm) coordinates across the two groups.

Measurements of PT volume were performed on MRIs using three-dimensional interactive pixel-labeling software that permits viewing in all three orthogonal planes of section simultaneously (17). Identification of the PT was performed after stereotaxic transformation of the MRIs into a standardized space (14) had been accomplished, thus controlling for overall differences in brain size or shape. Only voxels defined as belonging to gray matter according to MRI intensity values were labeled as PT tissue. This procedure yields estimates of cortical volume, rather than surface area, and is, therefore, relatively free of artifacts related to differential cortical folding. Criteria for definition of PT boundaries were as follows: the anterior border of the PT was formed by the sulcus posterior to the first Heschl's gyrus; the posterior border, which has often been problematic to identify (18), was defined as the point at which a discontinuity is observed from the temporal to the parietal plane in coronal sections. These criteria define the PT in a rule-based systematic fashion and avoid an arbitrary "knife-cut" that follows the angle of the Sylvian fissure (19). Measurements were performed blind with respect to side and subject group.

RESULTS

Behavioral Results. The behavioral data collected during scanning are shown in Table 1. Both groups performed the interval classification (minor/major) task adequately, but AP subjects performed significantly more accurately ($F_{1,18} = 9.53$, $P < 0.01$). No significant differences in latencies across groups were observed for the minor/major task.

Morphometry. Statistical analysis of the PT measures (Table 1) indicated no significant differences in PT volume between AP and RP groups, possibly because of the small sample size and large variability (Table 1). However, comparison of the PT volumes of the AP group with a larger sample ($n = 50$) of normal right-handed subjects unselected for musical skill (19) yielded a significant difference: the left PT was larger in the AP group (Mann–Whitney $U = 131$, $P < 0.03$), but the right PT was not (mean left and right PT volumes for the control sample: 4,238 and 4,156 mm^3, respectively). PT volumes in the RP group did not differ significantly from the large sample in either hemisphere.

Moreover, the relation between the size of the left PT and performance on the screening test among the subjects in both AP and RP groups yielded a significant correlation ($r = -0.39$, $P = 0.05$), indicating that larger PT volume was associated with lower error scores on the pitch-naming task.

PET Results. Comparisons of CBF data were performed by subtracting the noise condition from each of the two activation conditions, as a control for basic auditory and motor processes common to all conditions (9, 10). All significant increases in CBF are detailed in Tables 2 and 3, with the most relevant changes shown in Fig. 2. In the tones-minus-noise comparison, both AP and RP groups showed nearly identical loci of CBF increase (see Table 2), including the superior temporal gyrus bilaterally (Brodmann areas 22/42; Table 2, foci 4 and 5), and the right inferior frontal cortex (area 47/11; focus 3), as well as in the right occipital region (focus 7). The two groups showed a striking difference, however, in the left posterior dorsolateral frontal (DLF) region, close to the premotor cortex (area 8/6; focus 1), which was among the most significant activation foci in the AP group, but showed no trace of CBF change in the RP group (Fig. 2 *Top*).

In the minor/major-minus-noise subtraction (Table 3 and Fig. 2 *Lower*), the pattern of CBF increases for the AP group was comparable in some respects to the tones-minus-noise comparison, particularly in that the left posterior DLF area was again strongly activated; a mirror-image DLF focus in the right hemisphere (focus 3) was identified as well. In addition, bilateral increases were also seen in the superior parietal region (foci 8 and 9) and in the middle/inferior temporal cortex (foci 6 and 7; Fig. 2 *Lower*). In contrast to the tones-minus-noise subtraction, the AP group did not show any evidence of activation in the right inferior frontal cortex (focus 5; Fig. 2 *Lower*). For RP subjects, the minor/major-minus-noise subtraction resulted in a comparable pattern to that observed in the tones-minus-noise subtraction but with the important difference that significant CBF increases were observed this time in the left posterior DLF region (area 8/6), in a very similar position to those seen in the AP group (Table 3, focus 1, and Fig. 2 *Lower*). The pattern of other regions activated in the RP group in this subtraction was similar to that for the AP group, including bilateral activity within mid- and dorsolateral frontal areas, and in the parietal lobe. Inferior temporal regions (foci 6 and 7) also demonstrated bilateral increases for the RP group in locations very near those of the AP group; however, these foci failed to reach our standard level of significance for an exploratory search. There was one additional important difference between the two groups: a

Table 2. Foci of CBF increase in the tones-minus-noise subtraction

	AP group				RP group			
Area	*x*	*y*	*z*	*t*	*x*	*y*	*z*	*t*
1. L DLF	−38	3	48	4.45	—	—	—	
	−39	10	39	4.00	—	—	—	
2. L Mid-F	−40	27	18	3.91	−40	42	6	3.56
	−42	18	20	3.80				
3. R Inf-F	51	39	−9	3.69	35	49	−12	4.07
	15	34	−23	3.80				
4. L STG	−62	−1	−3	4.47	−59	−7	−2	3.25
5. R STG	52	−30	5	3.50	51	−18	9	3.37
6. L Parietal	−40	−61	47	3.93	−31	−45	33	3.88
7. R Occipital	31	−88	5	3.46	15	−87	29	3.41
					32	−73	17	4.04
8. L Cingulate	—	—	—		−17	−16	30	4.69

Stereotaxic coordinates refer to the atlas of Talairach and Tournoux (14). L, left; R, right; F, frontal; inf, inferior; STG, superior temporal gyrus.

Table 3. Foci of CBF increase in the minor/major-minus-noise substraction

	AP group				RP group			
Area	*x*	*y*	*z*	*t*	*x*	*y*	*z*	*t*
1. L DLF	−41	−1	45	5.19	−20	13	48	4.54
	−42	12	32	5.65	−42	6	29	4.62
	−44	15	24	5.09				
2. L Mid-F	−39	36	17	4.26	−25	32	12	3.46
3. R DLF	32	−2	53	4.31	16	18	48	3.75
	29	13	39	3.87				
4. R Mid-F	46	29	24	4.71	50	25	21	3.98
	31	32	21	4.09				
5. R Inf-F	—	—	—		36	55	−12	4.62
6. L Mid/Inf-T	−55	−50	−14	3.41	−58	−64	−11	2.90
7. R Mid/Inf-T	63	−45	−14	4.75	63	−50	−14	3.11
8. L Parietal	−36	−50	41	4.65	−32	−54	42	5.56
	−25	−57	36	4.53				
9. R Parietal	36	−49	39	4.17	42	−50	51	3.81
	43	−56	53	4.15				
10. Medial Sup-F	0	22	45	4.42	—	—	—	
11. L Midbrain	−4	−31	−21	4.29	—	—	—	
12. R Cerebellum	25	−78	−26	4.07	—	—	—	

Stereotaxic coordinates refer to the atlas of Talairach and Tournoux (14). Sup, superior; T, temporal. Other abbreviations are as in Table 2.

significant CBF increase was observed in the RP group in the right inferior frontal cortex (focus 5), in a nearly identical location to that seen in the tones-minus-noise subtraction (compare with Table 2, focus 3), but as noted above, this region did not demonstrate any CBF change in the AP group in the minor/major-minus-noise subtraction.

DISCUSSION

The PET data indicate both similarities and important differences in the neural processing of musical information in musicians with AP. The overall correspondence of CBF activity pattern across groups in both tones and minor/major conditions suggests that many aspects of the neural mechanisms involved in processing of tonal stimuli are common to AP possessors and control musicians. In particular, the foci of activation in the right superior temporal gyrus and right inferior frontal regions are similar to the activation locations reported in a previous PET investigation (10) among nonmusicians while listening to melodic patterns relative to noise bursts, implicating these regions in tonal processing. The superior temporal region is known to contain neurons that are sensitive to auditory stimuli; their response properties suggest that they are specialized for the analysis of certain acoustic features, including those relevant for music (20, 21). Because the control condition used for the subtraction consisted of acoustically matched noise bursts, the CBF changes observed are likely specifically related to the processing of tonal information (e.g., periodicity or spectral shape). Thus, AP would not appear to involve differences at the level of the initial stages of perceptual analysis, a conclusion consistent with the fact that early components of evoked potentials do not differ between those who do or do not possess AP (6–8, 22). It is also of interest to note that occipital areas showed increased CBF in both subject groups, despite the fact that no visual input was provided, a finding that parallels that of other PET studies (10, 23) and suggests that visual processing may be elicited by auditory stimuli under a variety of conditions.

The most remarkable difference between AP and RP groups in the tones-minus-noise comparison was the strong activation of the left posterior DLF cortex, which was observed only in the AP group. This portion of the frontal cortex has been implicated in conditional associative learning of sensory stimuli in both monkey and human (24, 25). Thus, lesions to this area impair the acquisition of arbitrary nonspatial associations between a stimulus and a particular response (24); moreover, PET studies show activation in the posterior DLF region during the performance of visual conditional associative learning tasks (26). AP may be characterized as the ability to retrieve an arbitrary association between a stimulus attribute (the pitch of a sound) and a verbal label, which is precisely the type of psychological process referred to as conditional associative learning above. Thus, the CBF increase in the posterior DLF cortex among the AP group but not the RP group while listening to tones may reflect the engagement of an associative mechanism. For AP possessors, such associations occur spontaneously and form the basis for AP labeling, whereas listeners without AP ability would be unable to label isolated tones and, therefore, show no activity in this region. This interpretation is consistent with the AP subjects' impression upon debriefing that during the tones condition, they were generally aware of the correct note names. The fact that the focus is situated in the left hemisphere would be consistent with the verbal nature of the association (26), in this case the note name (C-sharp, B-flat, etc.).

Although the left posterior DLF area was only active in the AP group in the tones condition, this same area was active in both groups in the minor/major condition. Thus, during a task that uses relative judgments, the RP group shows a similar pattern to the AP group in the DLF cortex. This pattern may also be explained by the hypothesis that DLF activation is related to verbal–tonal associations, because the interval classification task requires that the tonal stimuli be labeled (i.e., the relation between tones within a pair results in the verbal association of major or minor). The interval labels are themselves learned associations, but both AP and RP subjects would have access to them by virtue of their musical training (and the behavioral data shown in Table 1 confirm that both groups were generally successful at this task).

It is of interest that right DLF areas, symmetric to those discussed above, were also observed in the minor/major-minus-noise subtraction among both groups (Table 3). It may be that, in addition to tonal–verbal associations, this task elicits other nonverbal associations reflected by this bilateral activity. The availability of multiple sensory codes in AP musicians is supported by cognitive studies showing that blocking of verbal rehearsal has no effect on note-name retention among AP possessors (27), whereas verbal interference does affect re-

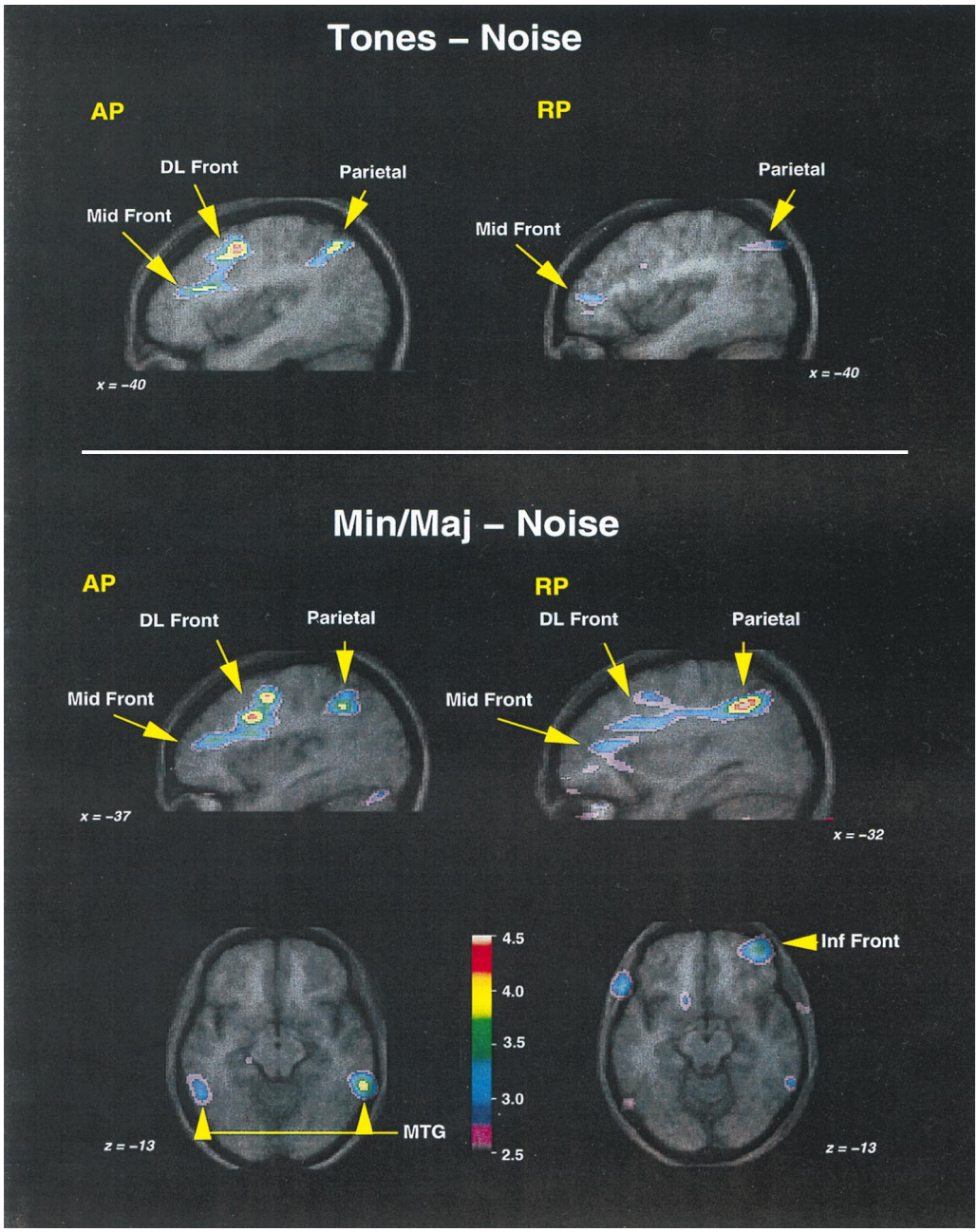

FIG. 2. (*Upper*) Averaged PET subtraction images are shown superimposed upon the averaged MRI scans for the tones-minus-noise subtraction for listeners with AP (*Left*) and control musicians—RP (*Right*). Focal changes in CBF are shown as a *t* statistic image, values for which are coded by the color scale at the bottom. The two saggital slices, taken at 40 mm to the left of midline, illustrate changes in the midfrontal and parietal regions, common to both groups (Table 2, foci 2 and 6), and a large focal area of CBF increase in the left dorsolateral (DL) frontal cortex (Table 2, focus 1), present only in the AP group (for stereotaxic coordinates and *t* values for these foci, see Table 2). (*Lower*) PET/MRI data for the minor/major-minus-noise subtraction for listeners with (*Left*) and without (*Right*) AP. The two saggital sections, taken at 37 and 32 mm to the left of midline, illustrate the similar CBF foci in the left DL frontal, midfrontal, and parietal regions for both groups of subjects (Table 3, foci 1, 2, and 8). The two horizontal sections, taken at 13 mm below the bicommisural plane, illustrate the right inferior frontal focus (Table 3, focus 5) present only in the RP group; foci within the middle temporal gyri (MTG) bilaterally are shown in the AP group but were also present, albeit more weakly, in the RP group (Table 3, foci 6 and 7; for stereotaxic coordinates and *t* values for these foci, see Table 3).

tention of purely verbal information, such as letters. The bilateral activation of middle/inferior temporal cortex (Brodmann area 21; Fig. 2 *Lower*) could also be related to recruitment of multiple codes, because these regions are thought to be involved in multimodal processing. The inferotemporal cortex is generally considered a visual processing area, (28) but it may also participate in visual–verbal associative functions (29). Its stronger activation in the AP group perhaps reflects their better access to multiple coding strategies (27).

In addition to the differential recruitment of the posterior DLF cortex across the two groups, a further dissociation is apparent, in that the right inferior frontal region (Brodmann area 47/11)—active in both groups in the tones-minus-noise comparison—shows no CBF change in the AP group (Fig. 2 *Lower*) in the minor/major condition. One possible interpretation of this finding is that activity in the right inferior frontal region, which is present only in the RP group in the minor/major condition, may reflect maintenance of pitch information in auditory tonal working memory. This conclusion is supported by functional imaging data (10, 30) that demonstrate CBF increases in similar right inferior frontal locations specifically during active pitch retention tasks. As well, behavioral

studies in patients with cortical excisions have also indicated that damage to the right frontal cortex impairs the ability to retain pitch information in working memory (31). We suggest that subjects without AP use tonal working memory in both tasks, but AP possessors may not need access to this mechanism for interval classification because they are able to classify each note within the interval by name. Thus, rather than compute the size of the musical interval itself based on its sound, which would require maintaining pitch in working memory, AP possessors may simply obtain the correct response by knowing what the individual notes are within the interval. This conclusion is concordant with the reported absence of the P300-evoked electrical component, specifically during an interval-judgment task similar to ours, among AP subjects (8). That result has been interpreted as reflecting the AP subjects' use of a long-term memory representation to accomplish the interval labeling task rather than needing to update working memory on every trial (6–8).

The morphometric measures of the PT yielded some evidence in favor of the hypothesis that AP may be associated with an anatomical difference in the left superior temporal area, as suggested by a prior study (4). In particular, our finding that left PT volume correlates with behavioral performance on a pitch-naming task provides direct evidence for the possible existence of a structure–function relationship. However, this result needs to be interpreted cautiously for several reasons. (*i*) Although the anatomical volumetric asymmetry in the AP group differed from that of the large reference group, they did not distinguish the AP from the RP group. (*ii*) There was no evidence of any CBF changes in or near the region of the PT in the functional data from either task. (*iii*) Finally, although our morphometric data are generally in the same direction as those of the previous investigation (4), they differ in that the previous study reported a difference in degree of asymmetry (as measured by a laterality index comparing left to right) but we find a difference in the left PT volume of the AP group only as compared with the size of the left PT in a large musically unselected sample. We did not find an exaggerated asymmetry *per se*; in fact, the right PT was also larger among the AP group than in the reference group, albeit not significantly so. These discrepancies may be related to a number of important methodological differences: notably, to our different definition of the PT boundaries, to the fact that we measured cortical volume rather than surface area, and to our use of stereotaxic normalization to control for overall differences in brain shape and size.

The findings of the present study suggest that no one regional activation pattern is unique to AP. Rather, the areas recruited depend upon the task demands, and the availability of specific processing mechanisms. In particular, the posterior DLF region would appear to play a key role in a distributed network related to the retrieval and manipulation of verbal–tonal associations. This network can also be used by musicians without AP, however, whenever associations can be made to the relation between pitches rather than to a single pitch. Although we did find evidence for a structural difference between AP possessors and a control sample in the left PT, the precise role played by this region remains to be determined. Nonetheless, it is important to note that the posterior portion of the superior temporal plane, including the PT, contains auditory association cortex (5) that projects directly to the most posterior portion of the DLF cortex (32), precisely the region that was strongly active in the AP group in both comparisons. It is therefore possible that AP arises from some qualitatively different neural process within the superior temporal region, as indexed by the differential morphology seen within the AP group. Why certain individuals possess AP remains unknown, but according to our view, AP may result from an interaction between computations in the superior temporal area and the engagement of a network of brain regions, particularly the posterior DLF cortex, involved in the retrieval and manipulation of various types of associations to the pitch of a tone.

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