

Separating pitch chroma and pitch height in the human brain

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Musicians recognize pitch as having two dimensions. On the keyboard, these are illustrated by the octave and the cycle of notes within the octave. In perception, these dimensions are referred to as pitch height and pitch chroma, respectively. Pitch chroma provides a basis for presenting acoustic patterns (melodies) that do not depend on the particular sound source. In contrast, pitch height provides a basis for segregation of notes into streams to separate sound sources. This paper reports a functional magnetic resonance experiment designed to search for distinct mappings of these two types of pitch change in the human brain. The results show that chroma change is specifically represented anterior to primary auditory cortex, whereas height change is specifically represented posterior to primary auditory cortex. We propose that tracking of acoustic information streams occurs in anterior auditory areas, whereas the segregation of sound objects (a crucial aspect of auditory scene analysis) depends on posterior areas.

Auditory scientists define pitch as the perceptual correlate of acoustic frequency: a single physical dimension along which musical notes can be ordered from low to high (1). However, humans perceive the notes of the scale as repeating once per octave; accordingly, music psychologists represent pitch as a helix (Fig. 1*a*) with a circular dimension of pitch chroma and a vertical dimension of pitch height (2–5). The function of these two pitch dimensions is illustrated when the same melody is sung by a male or female voice or played by a violin or cello. The vocal cords of women vibrate faster than those of men, and the strings of a violin vibrate faster than those of a cello. These physical differences correspond to differences in pitch height that contribute to our perception that women's voices are higher than men's, and violins are higher than cellos. Note this distinction is not based on pitch chroma, because both voices or instruments can produce the full range of chromas; it is an average pitch height difference that is more properly associated with the perception that one source is higher than another. Whereas pitch chroma is used in tracking the information conveyed by a particular sound source, pitch height is used in the segregation of sources. This study describes a functional MRI (fMRI) experiment designed to establish whether separate mechanisms for processing the two pitch dimensions exist in the human brain.

Previous human fMRI experiments have shown that pitch information is processed in regions beyond primary auditory cortex (PAC). PAC is located in the medial portion of Heschl's gyrus (HG) (6); musical melodies (7–9) and speech information (10, 11) activate areas that are lateral and anterior to PAC. Other functional imaging experiments indicate that the human planum temporale (PT) (12) posterior to HG is involved in auditory object segregation (13). However, the chroma and height dimensions of pitch have not been separated in previous functional imaging studies. We therefore designed the present fMRI experiment to determine whether the helical model of pitch perception is reflected in the organization of the human brain. We tested the specific hypothesis that pitch chroma changes (auditory information streams) are processed in anterior audi-

tory regions, and pitch height changes (changes in sound source identity) are processed in posterior auditory regions.

Methods

Bases for the Manipulation of Pitch Dimensions. In this experiment, we used stimuli in which pitch chroma and pitch height could be varied independently. The stimuli were harmonic complexes in which chroma and height could be varied continuously, whereas the total energy and spectral region remained fixed (Fig. 1*b*; examples are published as .wav files in the supporting information on the PNAS web site, www.pnas.org) (14, 15). The standard stimulus with all harmonics of the fundamental frequency, f_0 (Fig. 1*b Top*), had the pitch f_0 by definition. The pitch chroma of the stimuli was altered by varying f_0 in semitone steps as in the chromatic musical scale; this corresponds to motion around the pitch helix (red line in Fig. 1*a*). The pitch height was varied independently of chroma by reducing the amplitude of all odd harmonics in the complex (Fig. 1*b Middle*). If the odd harmonics of a harmonic complex are attenuated between 0 and ≈ 40 dB, relative to baseline intensity, the new tone has the same pitch chroma, f_0 , but is perceived as being higher in pitch; this change occurs along the pitch height dimension (blue line in Fig. 1*a*). When the odd harmonics are attenuated completely pitch height reaches the octave, $2f_0$ (Fig. 1*b Bottom*), and repeating the attenuation process over successive octaves produces continuous pitch height changes without concomitant chroma changes. Using this procedure, we were able to synthesize sequences of notes in which chroma and/or height could be independently varied between notes in the sequence (examples are available in the supporting information on the PNAS web site).

Relationship Between Pitch Height, Tone Height, and Timbre. There are at least three methods for producing a sequence of harmonic sounds that all have the same pitch chroma but which are heard to rise along a perceptual dimension as the sequence progresses (14). The rise can be achieved by varying the spectral envelope of the sounds or by changing the spectral fine structure (either the intensity or the phase of alternate harmonics). Such manipulations are all related to the type of increase one hears when the speaker changes from a man to a woman, or the instrument changes from a cello to a violin. All three manipulations have been described as producing an increase in tone height. Here, we consider tone height in a more restricted sense to refer to manipulation of the spectral envelope, which is more closely associated with timbre perception. In contrast, we use pitch height in this experiment to refer to a manipulation of spectral fine structure that is more closely associated with pitch perception.

Tone height manipulations associated with timbre are related to the size information in natural sounds (16). Women have

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Abbreviations: fMRI, functional MRI; HG, Heschl's gyrus; PAC, primary auditory cortex; PP, planum polare; PT, planum temporale; f_0 , fundamental frequency.

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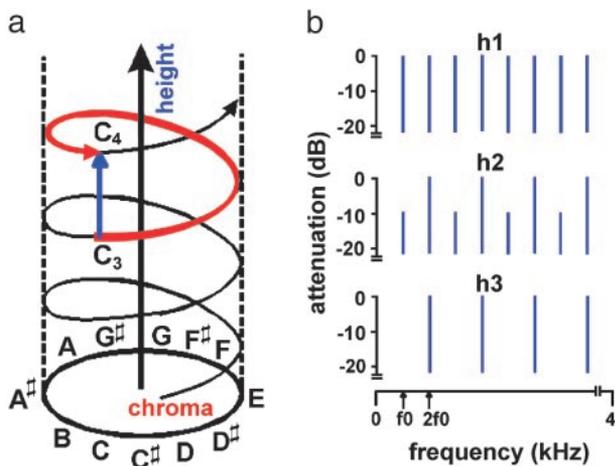


Fig. 1. (a) The pitch helix. The musical scale is wrapped around so that each circuit (red) is an octave. The equivalent change in pitch height with fixed chroma is shown (blue). (b) Examples of sounds with changing pitch height. Each of these harmonic complexes (h1, h2, h3) has a flat spectral envelope in the frequency band 0–4 kHz. In h1 (Top), all harmonics of the fundamental, f_0 , have equal amplitude; in h2 (Middle), the odd harmonics are attenuated by 10 dB, producing a large increase in pitch height without changing pitch chroma; in h3 (Bottom), the odd harmonics are completely attenuated, producing a one-octave rise in pitch height with the same chroma ($2f_0$).

shorter vocal tracts than men and, as a result, their formant frequencies are higher. Violins are smaller than cellos and, as a result, their resonant peaks occur at higher frequencies. The important point is that these tone height manipulations are associated with a dimension of timbre perception that is separate from pitch height, and the manipulations in the current experiments do not involve tone height in this sense. Pitch height manipulations are also related to the size information in natural sounds. These manipulations involve attenuation of the odd harmonics, as described above, or a fixed shift in the phase of either the odd or the even harmonics. The phase manipulations are noteworthy inasmuch as they have no effect on the power spectrum of the stimulus, but they still produce a rise the perceived pitch (14). This report is primarily concerned with the perception of pitch height rather than tone height and the location of pitch height processing rather than tone height processing in auditory cortex.

It is the case that manipulation of the fine spectral structure of sounds can also affect the timbre of a sound. For example, the characteristic timbre of a clarinet is partly due to the fact that the even harmonics are attenuated relative to the odd harmonics, which imparts a characteristic hollowness to the sound. In the current experiment, however, it was the odd harmonics that were attenuated (relative to the even harmonics), which has much less effect on the timbre of the sound. In summary, the manipulation of the spectrotemporal structure of the stimulus can have two perceptual effects, but it is the effect on pitch height that is the focus of the present paper. In the next section, we demonstrate ordering effects that are most parsimoniously explained in terms of a pitch dimension.

Psychophysical Effect of Pitch Height Manipulation. The effect of attenuating the odd components of a harmonic series on the pitch height of the sound was originally investigated in a scaling experiment (14, 15). We performed a new pitch height discrimination experiment to confirm that the stimulus manipulations used in the present study could be ordered continuously along the dimension of pitch height and to determine the resolution of discrimination along this dimension. In a two-interval two-

alternative forced-choice task, three normal subjects were presented with a standard stimulus and a test stimulus in which the odd harmonics were attenuated more than the standard; the task was to choose the stimulus with the higher pitch height. Notes all had the same pitch chroma (80 Hz), duration (200 ms), fre-

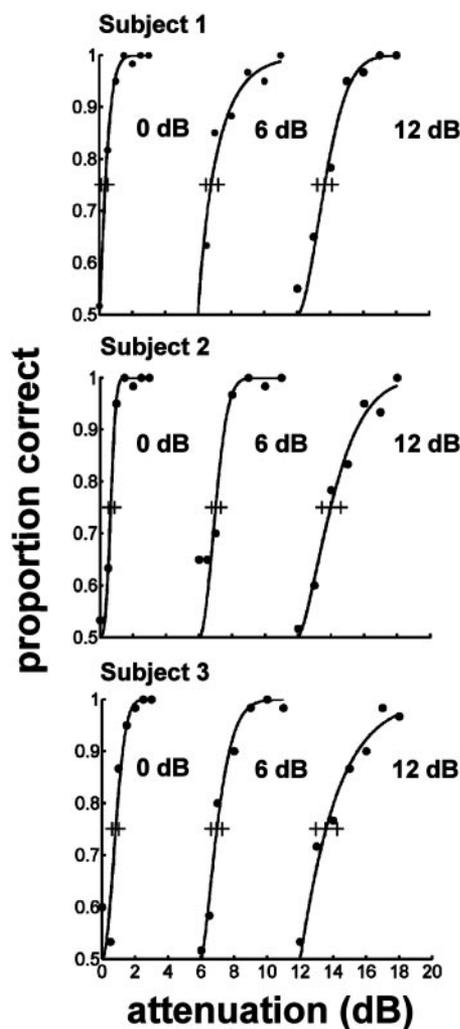


Fig. 2. Psychometric functions for pitch height. The psychometric function shows the dependence of the proportion of correct responses on the size of the change in pitch height. Psychometric functions for three subjects were derived from a two-interval two-alternative forced-choice experiment in which subjects were asked to detect which note is higher. The ordinate shows the proportion of correct subject responses, where 50% is equivalent to performance at chance; the abscissa shows the attenuation of odd harmonics in the test stimulus relative to baseline intensity. The fundamental frequency, f_0 , was fixed at 80 Hz throughout the experiment (see Methods). The psychometric functions are based on change in attenuation of odd harmonics relative to standards in which the odd harmonics have fixed attenuation of 0 dB (Left), 6 dB (Center), and 12 dB (Right). Each data point is based on at least 60 trials. Weibull functions were fitted by using maximum likelihood estimation implemented in MATLAB [Mathworks (Natick, MA) (fitting software at <http://bootstrap-software.org/psignifit>)]. The 75% threshold is defined as the attenuation value at which subjects achieve a score of 75% correct (halfway between chance and ceiling performance); the 75% thresholds and 95% confidence intervals for each threshold shown (+) were derived by using bootstrapping with 999 simulations (17, 18). To obtain 95% confidence intervals, the bootstrapping procedure used a Monte Carlo method for estimating the variability of the fitted psychometric function. All subjects heard an increase in pitch height from the standard when the odd harmonics were attenuated by ≈ 1 dB in the test stimulus, and the pitch height threshold is uniform along the dimension.

quency region (f_0 to 4 kHz), and energy (sound pressure level 70 dB). Three different standard stimuli were used for each listener where the odd harmonics had a fixed attenuation of 0, 6, or 12 dB. The results are presented in Fig. 2. The left-hand psychometric functions show how discrimination increased with attenuation for the standard with 0-dB attenuation of the odd harmonics. All three listeners had thresholds of <1 dB of attenuation and achieved near-ceiling performance at just over 2 dB of attenuation. The central and right-hand psychometric functions show that pitch height discrimination remained excellent and essentially uniform when the standard stimulus had fixed attenuation of odd harmonics by 6 or 12 dB. The experiment was performed without feedback and required essentially no training, indicating that the pitch height cue is stable and the direction of “higher” is consistent across listeners.

Stimulus Details. In the fMRI experiment, sounds were either pitch-producing harmonic complexes or broadband Gaussian noise (Fig. 1*b*; examples are published as supporting information on the PNAS web site). All stimuli were created digitally at a sampling rate of 44.1 kHz. Total energy and passband (0–4 kHz) were fixed for all stimuli. All sound sequences were 8 sec in duration; each sequence was composed of 40 individual sounds, each 200 ms in duration. The harmonic complexes were in cosine phase with components ranging from f_0 to 4 kHz (Fig. 1*b*). Pitch chroma was varied randomly across one octave (60–120 Hz) of the chromatic musical scale by varying f_0 from note to note in the sequence, in semitone steps. Pitch height was also varied randomly across approximately one octave, by attenuating the amplitude of all odd harmonics (Fig. 1*b Middle*) from note to note, in 2-dB steps. The note with the lowest pitch height had fundamental f_0 with 10-dB attenuation of the odd harmonics of f_0 ; the note with the highest pitch height had fundamental $2f_0$ with 10-dB attenuation of the odd harmonics of $2f_0$. The intervening pitch height steps had 12-, 14-, 16-, 18-, and 20-dB attenuation of the odd harmonics of f_0 and 0-, 2-, 4-, 6-, and 8-dB attenuation of the odd harmonics of $2f_0$. In the stimuli with

changing pitch height, chroma values were lowered by half an octave. The total range of subjective pitch change across a sequence was therefore approximately one octave, with either chroma variation or height variation, and the maximum overall pitch range was one-and-a-half octaves if both chroma and height variation occurred together.

Scanning Protocol. Ten subjects aged 21–38 (six males, four females; nine right handed, one left handed) participated in the fMRI experiment. None had any history of hearing or neurological disorder, and all had normal structural MRI scans. All subjects gave informed consent, and the experiment was carried out with the approval of the Institute of Neurology Ethics Committee, London. Before scanning, subjects were asked to pay attention to the sound sequences; to help maintain alertness, they were required to make a single button press at the end of each broadband noise sequence by using a button box positioned beneath the right hand and to fixate a cross in the middle of the visual field. There was no active auditory discrimination task. During scanning, six stimulus conditions were used, corresponding to six types of sound sequence: (i) fixed pitch chroma, fixed pitch height; (ii) changing pitch chroma, fixed pitch height; (iii) changing pitch height, fixed pitch chroma; (iv) changing pitch chroma, changing pitch height; (v) broadband noise without pitch; and (vi) silence. The order of conditions was randomized. Stimuli were delivered by using a custom electrostatic system (www.ihr.mrc.ac.uk/caf/soundsystem) at a sound pressure level of 70 dB. Each sound sequence was presented for a period of 8 sec, after which brain activity was estimated by the fMRI blood oxygen-level-dependent response at 2 T (Siemens Vision, Erlangen, Germany) by using gradient echo planar imaging in a sparse acquisition protocol (time to repeat/time to echo, TR/TE = 12,000/40 ms) (19). One hundred ninety-two brain volumes were acquired for each subject (32 volumes for each condition) in two sessions. Each brain volume comprised 48 contiguous transverse slices with an in-plane resolution of 3×3 mm.

After scanning, all subjects underwent two alternative forced

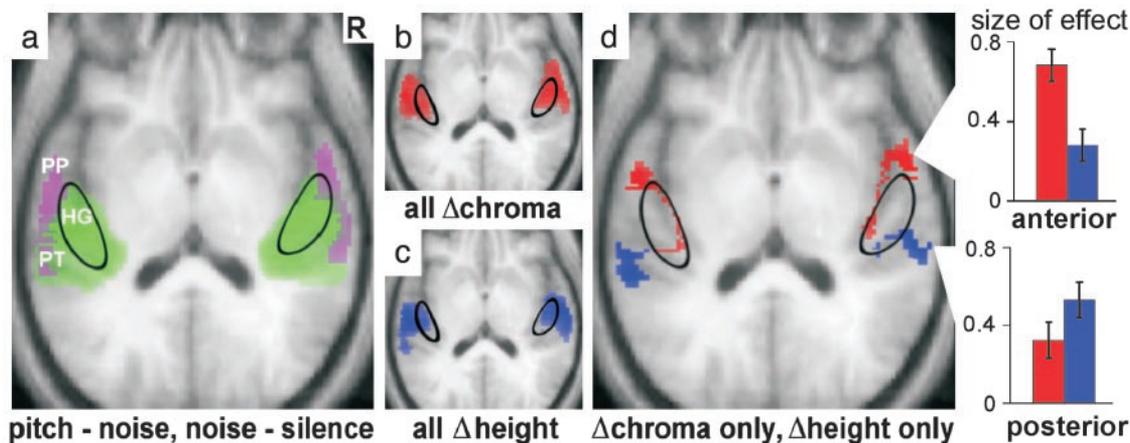


Fig. 3. Statistical parametric maps for the group. For each contrast (indicated below panels), activated voxels are rendered on the normalized group mean structural MRI in an axial section tilted 0.5 radians to include much of the surface of the superior temporal plane. The statistical criterion was $P < 0.05$ corrected for multiple comparisons across the whole brain volume. The 90% probability boundaries for PAC (6) are outlined (black). (a) Broadband noise contrasted with silence (noise–silence, green) activates extensive bilateral superior temporal areas including both medial and lateral HG. The pitch-producing stimuli contrasted with noise (pitch–noise, lilac) produce more restricted bilateral activation in lateral HG, PP, and PT. (b) Pitch chroma change contrasted with fixed chroma (all Δ chroma, red) activates bilateral areas in lateral HG, PP, and anterolateral PT. (c) Pitch height change contrasted with fixed height (all Δ height, blue) activates bilateral areas in lateral HG and anterolateral PT. (d) Voxels in *b* and *c* activated both by pitch chroma change and pitch height change have been exclusively masked. Pitch chroma change but not height change (Δ chroma only, red) activates bilateral areas anterior to HG in PP; pitch height change but not chroma change (Δ height only, blue) activates bilateral areas in posterior PT. These areas represent distinct brain substrates for processing the two musical dimensions of pitch. The relative magnitude of the blood oxygen-level-dependent signal change in anterior and posterior areas is shown for each of the contrasts of interest (Right). The height of the histogram columns represents the mean size of effect (signal change) relative to global mean signal for the contrasts Δ chroma-only (red) and Δ height-only (blue) at the peak voxels for each contrast in the right hemisphere; vertical bars represent the standard error of the mean size of effect. The histograms demonstrate opposite patterns of pitch chroma and pitch height processing in anterior and posterior auditory areas.

choice psychophysics to determine thresholds for detection of chroma and height changes in the sound sequences used during image acquisition. During scanning, the minimum pitch chroma and pitch height steps were one semitone and 2 dB, respectively. All subjects in the fMRI experiment could readily detect the changes in pitch chroma and pitch height and distinguish chroma sequences and height sequences; all had a threshold for detection of pitch chroma change less than one semitone and a threshold for pitch height change <2 dB. The sound sequences with changing pitch height were perceived by subjects as a disrupted auditory stream.

Image Analysis. A group analysis for all subjects was carried out by using statistical parametric mapping implemented in SPM99 software (www.fil.ion.ucl.ac.uk/spm). Scans were first realigned and spatially normalized (20) to the Montreal Neurological Institute standard stereotactic space (21). Data were spatially smoothed with an isotropic Gaussian kernel of 8 mm full width at half maximum. Statistical parametric maps were generated by modeling the evoked hemodynamic response for the different stimuli as boxcars convolved with a synthetic hemodynamic response function in the context of the general linear model. A fixed-effects model was used to assess differences in blood flow between conditions of interest (i.e., areas in which pitch chroma change and pitch height change produced additional activation to that produced by the fixed chroma and fixed height baseline conditions). The t statistic was estimated for each voxel at a significance threshold of $P < 0.05$ after correction for multiple comparisons across the whole brain volume according to Gaussian random field theory. Individual analyses were also carried out for each subject by using the same preprocessing parameters and statistical model and assessed by using a significance threshold of $P < 0.05$ after small volume correction taking the *a priori* anatomical hypotheses into account. For the contrast between changing and fixed chroma conditions, anatomical small volumes were derived from the group mean structural MRI brain; these small volumes comprised left and right lateral HG and planum polare (PP). For the contrast between changing and fixed height conditions, anatomical small volumes were based on 95% probability maps for the left and right human PT (12).

Results

Group Analysis. In the group analysis, significant activation was demonstrated in each of the contrasts of interest at the $P < 0.05$ voxel level of significance after correction for multiple comparisons across the entire brain volume. The contrast between broadband noise and silence produced extensive bilateral superior temporal activation, including medial HG and parts of PT (Fig. 3*a*, green) that was largely symmetric. The contrast between pitch conditions and noise produced more restricted bilateral activation in the lateral part of HG and PT and extending into PP (Fig. 3*a*, lilac). The contrasts between changing and fixed pitch chroma (Fig. 3*b*, red) and between changing and fixed pitch height (Fig. 3*c*, blue) produced common bilateral activation in lateral HG and anterolateral PT. Masking was then applied to exclude voxels activated by change both in pitch chroma and pitch height (Fig. 3*d*). Brain areas activated only by changes in pitch chroma were distinct from those activated only by changes in pitch height; pitch chroma change (Fig. 3*d*, red) produced additional activation extending anteriorly from HG into PP, whereas pitch height change (Fig. 3*d*, blue) produced additional activation extending posteriorly in PT. Activation was bilateral and slightly asymmetric; the activity in the right hemisphere was slightly more anterior than that in the left hemisphere. Local maxima of activation in the superior temporal plane for the group are listed in Table 1. The relative magnitude of the mean size of effect (change in blood oxygen-level-dependent signal) in each of the contrasts of interest (Fig. 3*d*

Table 1. Local activation peaks: Group data

Contrast	Region	Side	Peak, mm			Z score
			x	y	z	
Δ chroma only	PP	Left	-58	-2	-2	>8
		Right	60	0	-6	>8
Δ height only	PT	Left	-52	-6	4	6.76
		Right	-62	-30	10	7.74
		Right	66	-26	12	7.43

Coordinates for local peaks of activation in the superior temporal plane identified for the group. Coordinates correspond to voxels activated by pitch chroma change but not by pitch height change (Δ chroma only) or by pitch height change but not by pitch chroma change (Δ height only). Three-figure coordinates are in millimeters after transformation into standard MNI stereotactic space (21). Z score > 4.66 corresponds to $P < 0.05$ after correction for multiple comparisons across the entire brain volume.

Right) shows the opposite pattern for pitch chroma and pitch height processing in anterior and posterior auditory areas.

Individual Analyses. Individual subject analyses were carried out to determine whether the anatomical distinction between the re-

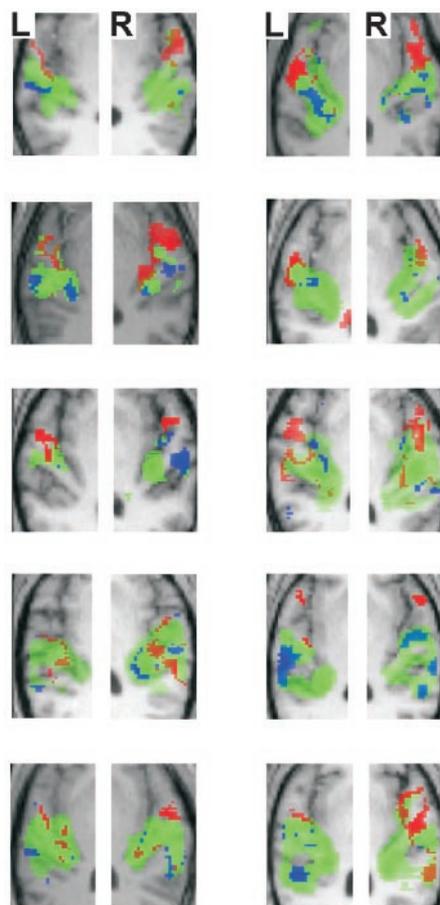


Fig. 4. Statistical parametric maps for individual subjects. Activated voxels ($P < 0.001$ uncorrected) are rendered on each individual's structural MRI. The axial section is tilted to run along the superior temporal plane as in Fig. 3, and the contrasts and color key are the same as in Fig. 3*a* and *d*. Bilateral areas including medial HG are activated in the contrast between broadband noise and silence (green). After exclusive masking of voxels activated by both pitch chroma change and pitch height change, the two pitch dimensions show distinct activation patterns in most individuals: pitch chroma change (but not pitch height change) activates mainly areas anterior to HG on the PP (red); pitch height change (but not pitch chroma change) activates mainly PT (blue).

gions specific for pitch chroma and height processing in the group was also evident in the individual data. Fig. 4 presents the individual results for the same axial slice as in Fig. 3; the pattern of activation in individuals was very similar to that of the group. An analysis was performed by using anatomical volumes of interest for lateral HG, PP, and PT specified *a priori* (see *Methods*). As in the group analysis, voxels activated both by pitch chroma change and pitch height change were exclusively masked to identify voxels specifically activated by pitch chroma change or pitch height change. There was significant activation in each contrast in all subjects at the $P < 0.05$ voxel level of significance after correction for the specified volume. For pitch chroma change, significant local maxima occurred in the prespecified volume involving lateral HG and PP in every subject. For pitch height change, local maxima occurred in the prespecified volume involving PT in every subject. Coordinates of local maxima for all individuals are in Table 2, which is published as supporting information on the PNAS web site.

Discussion

In this paper, we have presented psychophysical evidence to support the view that pitch has two distinct dimensions: pitch chroma and pitch height. When chroma is kept constant, pitch height can be manipulated and ordered from low to high along a continuous dimension. We have shown that the dimensions of pitch chroma and height have distinct representations in human auditory cortex. These representations occur at a logical point in the recently proposed hierarchy of melody processing (8, 9). Medial HG (PAC) is activated similarly when processing noise or pitch. Lateral HG (secondary auditory cortex) shows an increase in activity when processing pitch (Figs. 3 and 4), and it is activated by changing both pitch chroma and pitch height. Areas specifically activated by chroma change exist anterior to HG within PP, whereas areas specifically activated by height change exist posterior to HG within PT.

The analysis of pitch variation in sound sequences extending over seconds is required to process melodies in music and prosody in speech, and it has previously been shown to involve bilateral auditory areas anterior and posterior to HG (8, 9). However, these previous studies did not manipulate the two dimensions of pitch separately and did not address the possibility

that distinct brain mechanisms exist for the processing of pitch chroma and height. The pitch height changes in the present experiment were perceived by subjects as a disrupted auditory stream; here, pitch height provided a nonspatial cue for the segregation of sound objects at an early stage in auditory source analysis (22). Previous work showing activation in PT where spatial cues were the basis for segregation can be interpreted in a similar way (23). A specific mechanism for pitch height processing in PT is therefore in accord with a recently proposed model in which this area plays a critical early role in the segregation of sound objects in the acoustic environment (13). In contrast, specific activation of PP anterior to HG by stimuli with changing chroma supports previous work on melody (7–9) and speech (10, 11) processing; activation of anterior auditory areas would afford a mechanism for tracking pitch chroma patterns forming coherent information streams that can be analyzed independently of the specific sound source.

The anatomical and functional organization of the cortical auditory system in both humans and nonhuman primates is controversial (24, 25). In non-human primates, anatomical and electrophysiological evidence (26–28) suggests distinct what and where streams of processing beyond PAC, passing anteriorly and posteriorly, respectively. However, a proportion of neurons in the macaque posterior temporal lobe demonstrate responses to particular call sounds (28). In humans, functional imaging (29–31) and lesion (32) data support a dual organization beyond PAC; however, both the extent and the functional basis of any separation of processing mechanisms have been disputed (23–25). The present human study has demonstrated that mechanisms for analyzing pitch chroma patterns exist in the anterior temporal lobe, whereas mechanisms for analyzing pitch height exist in the posterior temporal lobe. If, as we hypothesize, pitch height differences are involved in the initial stages of auditory scene analysis, then it would seem reasonable to propose that in the human auditory brain, anterior cortical areas are engaged in processing patterns of information from one sound source, whereas posterior cortical areas are engaged in the segregation of sound sources in the environment.

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