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Localization of cerebral activity during simple singing

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CEREBRAL blood flow (CBF) was measured with PET during rudimentary singing of a single pitch and vowel, contrasted to passive listening to complex tones. CBF increases in cortical areas related to motor control were seen in the supplementary motor area, anterior cingulate cortex, precentral gyri, anterior insula (and the adjacent inner face of the precentral operculum) and cerebellum, replicating most previously seen during speech. Increases in auditory cortex were seen within right Heschl's gyrus, and in the posterior superior temporal plane (and the immediately overlying parietal cortex). Since cortex near right Heschl's has been linked to complex pitch perception, its asymmetric activation here may be related to analyzing the fundamental frequency of one's own voice for feedback-guided modulation. *NeuroReport* 10:3979–3984 © 1999 Lippincott Williams & Wilkins.

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Introduction

Singing is a highly evolved, uniquely human ability that involves volitional control of vocal fundamental frequency. In singing (without words), this control is most crucially directed towards the vocal fold movements responsible for fundamental frequency control [1]. The pattern of fundamental frequency variation in sung utterances is typically organized around a series of relatively steady-state segments (or notes), each of which expresses a single musical pitch. Although a number of studies have used PET to map brain regions associated with speech [2–5], this is the first to our knowledge to examine similar increases during singing.

In contrast to other primates, lateral neocortical control of vocalization is much more prominent in humans. Direct electrical stimulation of exposed cortex in the pre- and post-central gyri can produce vocalizations in humans, described as sustained vowel cries. Electrical stimulation of the supplementary motor area (SMA) can also produce vocalization in humans. So can stimulation of the immediately subjacent anterior cingulate cortex (ACC) in the dorsal bank of the cingulate sulcus. Vocalization from ACC has been reported following stimulation of the cingulate gyrus from just ventral to the SMA up to the dorsal bank of the cingulate sulcus. These medial frontal-evoked vocalizations tend to be rhythmically interrupted, rather than sustained cries [6]. Thus, based on the results of electrical stimulation mapping, increases in CBF during rudimentary singing were expected within at least the following cortical regions: (1) the precentral gyri, (2) the supplementary motor area (SMA), and (3) the anterior cingulate cortex (ACC).

Thirteen normal volunteers participated in two scanning conditions. In the first condition (Singing), they vocalized a single pitch repeatedly. In an auditory baseline condition (Perception), they listened to complex tones presented at a similar rate and transposed to the same frequency range.

Materials and Methods

The thirteen volunteers were all right-handed, and included six men and seven women (average age 24 years, range 19–34). None had substantial training in music performance (average 1 year), or any formal voice or music theory training. All gave informed, written consent before participating in the experiment, and after its nature and possible consequences were explained to them. The study was approved by the Research Ethics Committee of the Montreal Neurological Institute and Hospital.

An easy, relaxed pitch was chosen by each subject. A target repitition rate of 1 note/1250 ms was rehearsed briefly before the scan be singing along with a series of 1250 ms complex tones (0 ms intertone interval) with the same fundamental frequency using the vowel \ä\ then continuing to sing the same pitch at approximately the same rate after the series of tones ended. Just before the scan a brief sample of the target pitch and rate was again presented. During Singing, subjects attempted to sing this pitch repeatedly using the vowel \ä\ for 60 s, pausing for breath as needed. This rudimentary form of singing could also be described as a simple form of chanting. The complex tones for Perception were produced by a Yamaha TX81Z synthesizer with a clarinet-like timbre, and presented binaurally through plastic tubes inserted into the ear canal at a sound pressure level of ~75 dB. The present singing data served as the sensorimotor control in a study of monitoring within tonal working memory [7]. The Perception condition involved listening to six-tone sequences similar to those used in the tonal working memory tasks, but with no task imposed. They were transposed to each subject's vocal range, and presented through insert earphones (Eartone Type 3A). During both conditions, subjects' eyes were closed. Each subject performed a total of seven scans within a single session, two of which are discussed in the present paper.

Details of the positron emission tomography procedures are identical to those described by Zatorre *et al.* [8]. PET scans were obtained with a Scanditronix PC-2048 tomograph that produces 15 brain image slices with an intrinsic resolution of $5 \times 5 \times 6$ mm. The regional distribution of cerebral bloodflow (rCBF) was measured using the $H_2{}^{15}O$ bolus method with 60 s scanning periods and minimum 10 min interscan intervals. In each scan, 30 mCi $H_2{}^{15}O$ were injected into the left antecubital vein. High-resolution MR images (63 slices, 2 mm thick) were obtained with a Philips 1.5 T Gyroscan and co-registered with the PET data. After establishing an orthogonal coordinate frame centered on the line connecting the anterior and posterior commisures [9], the MRI and PET data from each subject were linearly re-sampled into a standardized stereotaxic coordinate system [10]. Reliable focal changes in CBF were sought using a method based on 3-D Gaussian random field theory [11]. All such focal peaks with $t \geqslant 3.5$ were considered highly reliable, resulting in an uncorrected probability of $p < 0.0002$ (one-tailed). Individual MR images were similarly averaged, and the resulting averaged neuroanatomical and CBF change images were merged, permitting direct localization of regions of significant change, and their maximal, peak voxels (see Fig. 1).

Results

Behavioral performance: Quantitative behavioral data are available for six of the 13 subjects. All understood the task instructions, and were observed to carry them out, with varying degrees of fluctuation in pitch. Vocalizations were recorded by a microphone suspended above the subject's mouth. The fundamental frequency was derived from the microphone signal by a dedicated voltage to MIDI (musical instrument digital interface) converter (Pitchrider, IVL Technologies), and analyzed off-line by a program that determined the average pitch of the most stable portion of each sung note. During the 60 s scan, the range from the highest to the lowest pitch was 41–107 cents (or 100ths of a semitone), indicating that all succeeded in singing pitches that fell within a range of ~1 semitone from the target. The average inter-onset interval during the scan was overall a little slower than the target rate of 1250 ms (mean 1567 ms, range 1200–1935). However, the resulting number of sung notes during the scan (mean 39 notes, range 31–50) was comparable to the number of tones presented during perception (36 tones).

PET: The mean CBF change image volume expressed as a 3-D t-statistic volume, was derived for CBF during Singing minus Perception (see Fig. 1A–F). The resulting list of focal CBF increases (Table 1) presents the coordinate location and t-value of the maximum voxel within each region of statistically significant difference.

Motor areas: Regions of increased CBF in motor cortical regions were observed bilateraly in the face region of the central sulcus (Fig. 1C,D,E) and medially in the SMA and in the cingulate sulcus (Fig. 1B).

Two regions of activation were also observed that reached their maxima in insular cortex. The more robust peak in the left insula fell deep to the precentral gyrus (Focus 6, Fig. 1A), on the dorsal portion of the first long insular gyrus. Activated pixels were also observed in the same portion of the right insula (e.g. x, y, z: 38, 1, 8; $t = 4.5$) but the peak of this region fell in the immediately adjacent frontal operculum (Focus 4).

A distinct peak was also observed in the right insula (Focus 7) that fell considerably more posteriorly, on the upper portion of the second long insular gyrus. In the monkey, an analogous portion of the insula receives projections from posterior auditory cortex [12].

Robust, symmetrical peaks were observed bilaterally in the cerebellum.

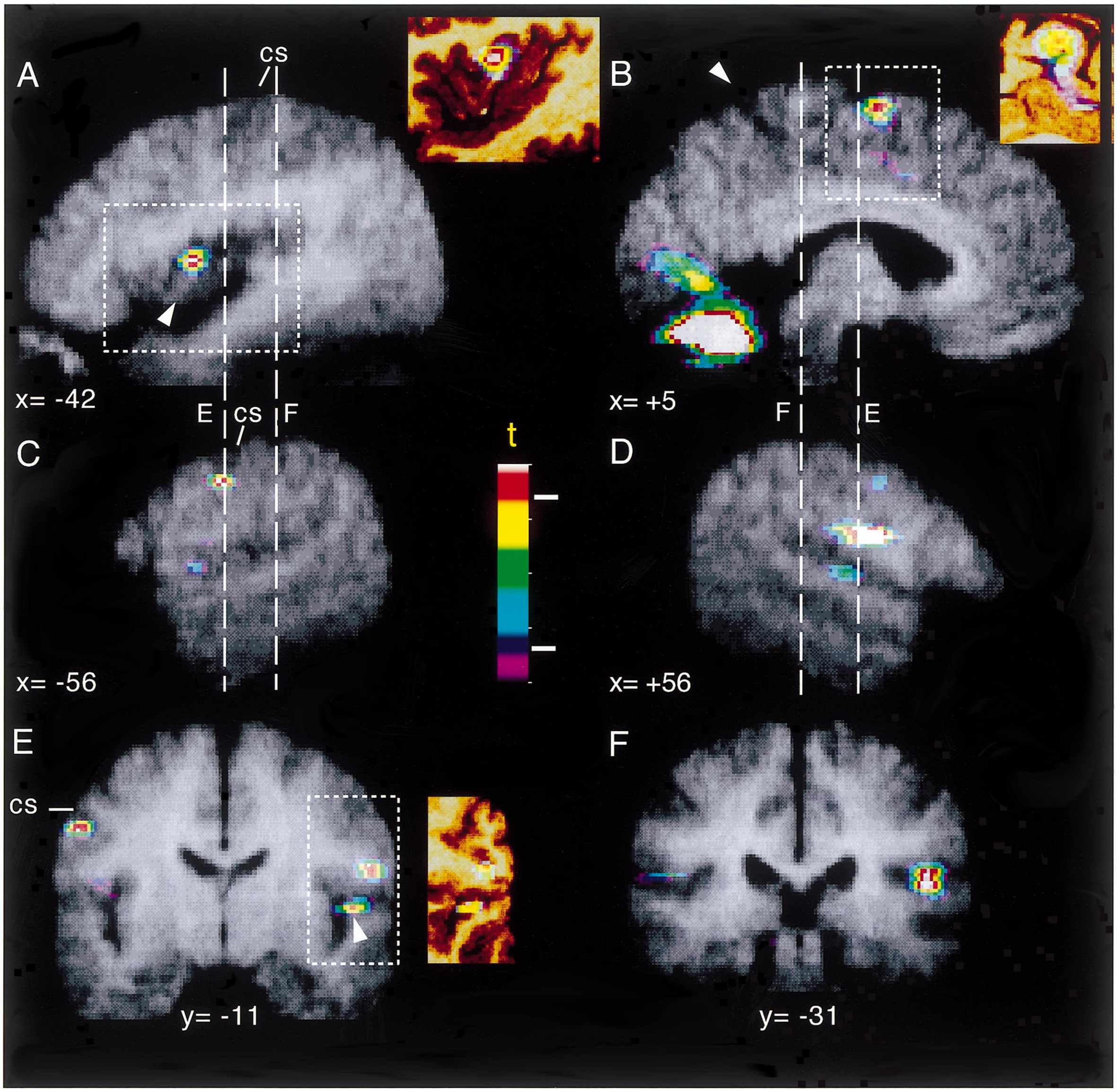

FIG. 1. Cerebral bloodflow during singing contrasted to auditory perception. Saggital (**A**,**B**,**C**,**D**), and coronal (**E**,**F**) slices from the CBF change t-statistic volume for Singing minus Perception, superimposed onto the averaged MRI (magnetic resonance image). Interrupted lines in the saggital slices indicate the planes of the two coronal slices. For saggital images, right hemisphere slices are on the right side of the figure. For coronal images, the right hemisphere is on the right half of the slice. CBF change data are thresholded for each slice so as to best view the location of the maxima of significant regions of increased CBF without obscuring the underlaid MRI data. The t ranges listed below for each image indicate the minimum value displayed as blue, and the mimimum value displayed as red, corresponding to the upper and lower hatch marks on the spectral color scale. In order to better interpret the averaged MRI data in crucial regions where the details of sulci and gyri are obscured by individual variability, the same rCBF data are shown superimposed on a randomly selected individual MRI resampled into the same stereotaxic coordinate system. The dotted rectangles in (A), (B) and (E) correspond to the regions shown on an individual MRI offset to the right. The focus numbers below correspond to the list of local maxima in Table 1. The statistical reliabilities of each region of increased CBF may best be compared across slices by examining the t values of the peak voxels in Table 1. Note however that the scales are identical for (C), (D) and (E). x coordinates refer to the distance in millimeters to the left (negative) and to the right (positive) of the mid-saggital commisural plane, y coordinates to the distance anterior or posterior to the coronal plane through the anterior commisure, and z coordinates to the distance above or below the horizontal commisural plane. Saggital slices: (A) $x = -42$ ($t = 5.45-6.06$) A peak of CBF increase (Focus 6) can be seen in the first long gyrus of the insula, indicated by the arrowhead, and visible more clearly in the individual MRI to the right. (B) $x = +5$ ($t = 3.2-4.17$) Significant maxima of CBF increase can be seen (from dorsal to ventral, i.e. top to bottom) in the supplementary motor area (Focus 1) and in the cingulate sulcus (Focus 5), seen more clearly on the individual MRI to the right. Note the marginal ramus of the cingulate sulcus [3], indicated by the arrowhead. Given the degree of individual variability in the position of these sulci [3], and the limits of measurement with PET, it cannot be concluded which bank the peak falls in, i.e. dorsal as it appears in the merged slice, or ventral, as it falls in the individual example. Visual cortex activation that is part of the right lingual peak (Focus 12) can also be seen. Most ventrally, activation is visible that is coextensive with more lateral peaks in the cerebellum (Focus 16). (C) $x = -56$ ($t = 5.03-5.7$) The left dorsal-most increase in the central sulcus can be seen (Focus 2). The position of the central sulcus (cs) at the dorsal edge of the slice is indicated, as it is in the more medial slice above (A). Proceeding ventrally, the next small group of activated voxels is part of the region whose peak lies more medially in the left ventral precentral gyrus/central sulcus (Focus 3). The next activated region is associated with the insular peak seen in (A). (D) $x = +56$ ($t = 5.03-5.7$) Both the dorsal and ventral activations along the right central sulcus can be seen (Foci 2 and 3). The activated voxels seen just below the Sylvian fissure are part of the region whose peak lies just medially on Heschl's gyrus. Coronal slices: (E) $y = -11$ ($t = 5.03-5.7$) A significant peak can be seen in the more dorsal left central sulcus (Focus 2), and in the ventral right central sulcus (Focus 3). Note that the left peak is the same as that depicted in (C), and the right as that depicted in (D). A significant peak can also be seen in right Heschl's gyrus (position indicated by the arrowhead; Focus 8), visible more clearly on the individual MRI data to the right. (F) $y = -31$ ($t = 3.81-4.78$) Significant peaks of CBF increase are seen in the right superior temporal plane (STP, Focus 9), and in left parietal cortex immediately overlying the STP (Focus 10). The pattern of CBF increase on the right suggests activation in both the STP and the overlying portion of the right parietal cortex.

Table 1. Foci of regions of increased cerebral blood flow (CBF) during singing, as compared to complex pitch perception

Brain area		Left hemisphere				Right hemisphere			
		x	y	z	t statistic	x	y	z	t statistic
Frontal lobe									
1. Supplementary motor cortex	6					0	−4	62	4.78
2. Precentral gyrus (dorsal)	4,6	−56	−11	36	5.88	60	−2	39	5.31
3. Precentral gyrus (ventral)	4,6,1	−50	−6	15	5.23	57	−4	20	6.31
4. Opercular premotor cortex		see 6				44	1	10	4.65
Cingulate gyrus									
5. Cingulate sulcus	24,32	3	6	40	3.50				
Insula									
6. Insular cortex (1st long gyrus)	–	−42	−1	8	6.32	see 4			
7. Insular cortex (2nd long gyrus)						39	−6	−6	4.25
Temporal lobe									
8. Heschl's gyrus	41,42					51	−11	6	5.72
9. Posterior superior temporal cortex	42	see 10				51	−30	15	5.37
Parietal lobe									
10. Inferior parietal cortex	[42]	−50	−33	18	4.33	see 9			
11. Angular gyrus	39					52	−69	12	3.51
Occipital lobe									
12. Lingual gyrus	18	−8	−97	−12	3.94	13	−62	3	5.11
13. Cuneus	18,19	−3	−78	15	3.83	23	−66	24	3.55
14. Calcarine cortex	17	−12	−78	2	4.42	11	−69	9	4.09
Brain stem									
15. Subthalamus	–	−11	−21	−8	4.77				
Cerebellum									
16. Cerebellar hemisphere (VIa)	–	−19	−59	−20	7.45	17	−57	−20	8.38

Auditory cortical areas: Two activation peaks were observed in the right superior temporal gyrus: one in the middle portion of Heschl's gyrus (Peak 7, Fig. 1E), i.e. in or near the right primary auditory region, and the other more posteriorly in the superior temporal plane, lateral to the posterior end of Heschl's gyrus (Focus 8, Fig. 1F). A peak was also found in the left inferior parietal lobe immediately superior to the analogous portion of the left posterior superior temporal plane (Focus 9, Fig. 1F). Activated pixels were found in the same portion of the right inferior parietal lobe, but were grouped as one region with Focus 8. Nevertheless, the distribution of activation within this region clearly suggests two adjacent cortical surfaces (see Fig. 1F).

Visual cortical areas: Foci were also observed bilaterally both in primary visual (calcarine) cortex and in visual association cortex above and below the calcarine fissure (cuneus and lingual gyrus). Part of the right lingual region can be seen in Fig. 1B.

Other peaks were seen in the angular gyrus of the right inferior parietal lobe, and in the brain stem just below the thalamus, i.e. near the red nucleus.

Discussion

Motor control: The location of the SMA focus (Focus 1) is virtually identical to some previous PET observations during simple speech output [2–4]. It corresponds to the face zone of 'SMA proper' in the cross-species neuroanatomical analysis of Picard and Strick [13].

The peak observed within the cingulate sulcus is similar in position to others seen during speech (Focus 5, Fig. 1B) [2–4]. However, most of those peaks fell either somewhat anterior or superior to this one, and only during tasks more complex than simple output [3]. The peak seen here may correspond to a lower level of vocal motor control. Its location, just ventral and anterior to SMA, is the same as one from which simple vocalizations have been elicited by electrical stimulation in humans [6].

The locations of the dorsal-most bilateral pair of peaks near the central sulcus (Foci 2, Fig. 1C,D,E) correspond well on the dorsal-ventral axis with the majority of peaks obtained during speech (i.e. $z = +32 - +42$) [2–5]. The location of the ventral-most pair of peaks (Foci 3, Fig. 1C,D,E) also corresponds to others reported during speech (i.e. $z = +20$) [2,5]. Both pairs fall within the orofacial zone of primary somatomotor cortex, near the somatosensory lip area as measured with PET (i.e. $z = +28$) [14]. Thus the locations of peaks in the region of the central sulcus during singing also appear to overlap those seen during speech.

It is not possible to entirely distinguish between activation of the pre- and post-central banks of the central sulcus, given the spatial resolution of PET. Therefore these regions of CBF increase could include both motor and somatosensory cortex. This is particularly likely within the cortical larynx representation, since vocal cord vibrations also result in somatosensory feedback. However, somatosensory activation in particular would be expected to be bilaterally symmetrical.

CBF increase was more robust in the right ventral-most precentral gyrus during singing (Fig. 1D). This asymmetry is consistent with a recent study that used functional magnetic resonance imaging to compare activation in the lower half of the precentral gyri during silent speech and silent singing. Significantly more pixels were activated in the right precentral gyrus during singing, and the left precentral gyrus during speaking, both in the same region activated bilaterally by tongue movements [15].

With regard to the peaks seen in the precentral gyrus of the insula, and the adjacent frontal operculum, it is worth noting that in the monkey paramotor cortex in the inner face of the precentral operculum receives projections from the adjacent mid-insular cortex [12]. If a similar topography exists in humans, then simultaneous activity in both areas could be expected, and, depending in large part on the filter size selected, might result in the measurement of a single region of activation whose peak could fall in either the insula or the operculum. Similar peaks in the left hemisphere have been observed during speech, and were initially described as buried Sylvian or opercular [4], or later as Sylvian-insular [16], though without PET–MRI correlation more precise anatomical localization was not possible.

A recent lesion analysis of stroke patients with apraxia of speech implicated a portion of the left insula as the only region affected in all such patients [17]. Its estimated location in Talairach coordinates (−41, −2, 10) corresponds strikingly to the left insular peak observed here during singing (Fig. 1A). Although its precise location was estimated as the precentral gyrus of the insula (i.e. the short gyrus just anterior to the central sulcus of the insula), its position seems indistinguishable from the one identified here (on the first long gyrus, just posterior to the central sulcus). Given the limits of measurement of both methods, the regions identified seem identical.

Interestingly, dysprosody is also one of the hallmarks of this disorder, and has been proposed to be either a result of, or a compensation for the deficit in articulation [17]. The present results suggest an alternative explanation: deficits in the control of vocal fundamental frequency and articulation may coexist because this region of the insula is critical for the production of all complex, volitional vocalizations. However, the present task involves singing a regular sequence of a single vowel, the articulatory demands of which may be sufficient to activate the left precentral gyrus.

The cerebellar peaks accord well with those seen during speech [2,4]. They correspond to lobule VIa [18]. Cerebellar activation is not surprising, since singing requires fine motor control, and patients with cerebellar lesions often demonstrate unsteady vocal pitch.

Auditory processing: In contrast to the motor system, where a condition with output was contrasted to one without output, in relation to the auditory system two different types of input were contrasted, one consisting of self-generated and the other of externally presented complex pitch. Interpretation of any increases related to the auditory system must take into account the greater complexity of this contrast. Any increases could, however, be related to unique processing demands imposed by self-generated sung input.

In their cytoarchitectonic analysis of three human brains, Galaburda and Sanides [19] found that part of the area they labeled posterior caudodorsal parakoniocortex (PaAc/d) continued upwards into the overlying parietal lobe. Thus both the peak in the left inferior parietal lobe and that in the right posterior superior temporal plane may represent activation of posterior auditory association cortex (i.e. PaAc/d). These regions of increased CBF in posterior auditory cortex fall within Wernicke's area and its right hemisphere analogue.

The tone sequence perception baseline would be expected to activate auditory cortex either bilaterally (in relation to silence) or with a right asymmetry (in relation to noise) [8]. The right-sided asymmetry of CBF increase in the primary auditory region during singing may reflect its specialization for complex pitch perception [20,21]. Accurate perception of the pitch of one's own voice is required during singing in order to use feedback to adjust and maintain an intended pitch. Corrective auditory feedback, in which an error signal between the target and the perceived pitch is minimized by muscle adjustments, has been proposed to be crucial for controlling vocal fundamental frequency [1]. Activation of more posterior auditory cortex might also be related to deriving vocal fundamental frequency, or to using it as feedback. However, these auditory increases could be related to any aspect of the difference between perceiving one's own voice while singing, and perceiving similar complex tones. Further experiments will be needed in order to elucidate the functional basis of these increases within auditory cortex in response to one's own singing voice.

A role has been proposed for connections between anterior cingulate cortex and auditory association cortex in the use of auditory feedback to modulate vocalization [22,23]. One function of interactions between vocalization-producing and auditory-decoding cortical areas may be to provide corollary feedback to the auditory-decoding regions about intended vocalizations, in order to facilitate either ignoring the resulting acoustic events (as seems plausible for speech) or focusing attention upon them [22,24] as seems necessary for singing.

Visual cortex activation: Increases in visual cortex were seen in spite of the fact that subjects' eyes were closed during both conditions. Occipital activation has also been reported during both speech [25] and melody [8] perception. Strategies involving cross-modal visual imaging of the auditory input might account for these activations. Alternatively, some more hard-wired cross-modal interaction may explain these increases within visual cortex, which might thus be incidental and not functionally relevant to the present task.

Conclusion

All of the cortical regions activated here may be understood to function as part of a complex distributed network for the production of singing. For example, projections exist in non-human primates from insular cortex to the premotor cortex of the precentral operculum [12], and may be involved in the planning of volitional vocalizations. Those between anterior cingulate and auditory association cortex [22,23] may be involved in the integration of motor planning and auditory feedback, as may those between anterior and posterior insula [12].

Overall, simple singing or chanting of a single vowel and pitch appears to activate many of the same regions as does speech. However, asymmetrical activation was noted in the right ventral precentral gyrus. Also, in contrast to a pitch perception baseline, singing resulted in greater activation in the right primary auditory cortical region. Thus, the cortical network activated by singing appears to be substantially similar to that previously reported during speech, but with some possibly opposite hemisphere asymmetries in both motor and auditory regions. Further analysis of differences in the networks involved, and of any hemisphere asymmetries within them, will have to await replication of the results for singing, and ultimately, more direct comparisons between singing and speaking.

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