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The brain basis of piano performance

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Abstract

Performances of memorized piano compositions unfold via dynamic integrations of motor, perceptual, cognitive, and emotive operations. The functional neuroanatomy of such elaborately skilled achievements was characterized in the present study by using ^{15}0-water positron emission tomography to image blindfolded pianists performing a concerto by J.S. Bach. The resulting brain activity was referenced to that for bimanual performance of memorized major scales. Scales and concerto performances both activated primary motor cortex, corresponding somatosensory areas, inferior parietal cortex, supplementary motor area, motor cingulate, bilateral superior and middle temporal cortex, right thalamus, anterior and posterior cerebellum. Regions specifically supporting the concerto performance included superior and middle temporal cortex, planum polare, thalamus, basal ganglia, posterior cerebellum, dorsolateral premotor cortex, right insula, right supplementary motor area, lingual gyrus, and posterior cingulate. Areas specifically implicated in generating and playing scales were posterior cingulate, middle temporal, right middle frontal, and right precuneus cortices, with lesser increases in right hemispheric superior temporal, temporoparietal, fusiform, precuneus, and prefrontal cortices, along with left inferior frontal gyrus. Finally, much greater deactivations were present for playing the concerto than scales. This seems to reflect a deeper attentional focus in which tonically active orienting and evaluative processes, among others, are suspended. This inference is supported by observed deactivations in posterior cingulate, parahippocampus, precuneus, prefrontal, middle temporal, and posterior cerebellar cortices. For each of the foregoing analyses, a distributed set of interacting localized functions is outlined for future test.

Keywords: Music performance; Piano performance; Functional neuroimaging; Music cognition

1. Introduction

Musical performance is very likely the domain in which humans produce the most intricate, complex integration of expert perceptual, motor, cognitive, and emotive skills. But although it may be the pinnacle of human central nervous system performance (and what space aliens most covet), its basis in the brain rarely has been investigated. Fortunately, musical ability and cognition appear to yield to fractionation (e.g., Peretz & Coltheart, 2003; Sergent, 1993), and components of musical performance have been studied with neurological, electrophysiological, and neuroimaging methods. These performance components include perception, sight-reading, motor-sensory processes, and attention.

The most deeply studied component is the neural basis of perceptual aspects of musical performance. Researchers have demonstrated, for example, strong associations amongst the strength of neurophysiological responses to pure tones in the musical range (detected via magnetoencephlography, MEG), the volume of anterior-medial Heschl's gyrus from which the responses originate, and musical skill (Schneider et al., 2002). Others have demonstrated enhanced neural representation for the timbre of the instrument in which a musician specializes, as compared to others (Pantev, Roberts, Schultz, Egnelien, & Ross, 2001) and the differences in the neural representation of musical pitch and rhythm between musicians and individuals with very little musical performance experience or training (Evers, Dannert, Rodding, Rotter, & Ringelstein, 1999; Parsons & Thaut, 2001). Studies have also

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examined the relation between auditory perception and motor behavior. Thus, one MEG study demonstrated that when pianists, but not singers, listen to familiar piano pieces to detect errors, they exhibited involuntary activations in cerebral cortical motor systems (Haueisen & Knosche, 2001).

Fewer functional brain investigations have targeted activities more intimately related to the production aspects of musical performances, which is the focus of the present paper. Various approaches have been used to investigate the sight-reading of musical scores. Several neurological case studies examined musicians' acquired impairments in sight-reading (Cappelletti, Waley-Cohen, Butterworth, & Kopelman, 2000; Judd, Gardner, & Geschwind, 1983; Marin & Perry, 1992; Sergent, 1993; Stewart & Walsh, 2001). Positron emission tomography (PET) has been used to study pianists sight-reading (Sergent, Zuck, Terriah, & McDonald, 1992), and to study conductors sight-reading a score as they detected errors in its heard performance (Parsons, Hodges, & Fox, 1998). More recently, MEG was used to investigate musicians imagining the musical sounds of a score they sight-read (Schurmann, Raij, Fujiki, & Hari, 2002). These studies and others (e.g., Nakada, Fujii, Suzuki, & Kwee, 1998; Schon, Anton, Roth, & Besson, 2002; Stewart et al., 2003) suggest that a core distributed network of areas in parietal, temporal, and occipital cortices support sight-reading, with other areas in frontal, sub-cortical, and cerebellar areas, being recruited depending on whether the score is merely read, read and imagined to be heard, or read while being performed.

A variety of research has focused on sensorimotor processes related to performing on musical instruments. MEG studies indicate that the extent of cortical representations for musicians' digits is related to the degree of skilled performance with those digits, as well as to the age at which the musicians started training on the musical instrument (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). Such functional differences are complemented by anatomical MRI studies reporting increased size and specific structural differences in musicians, as compared to non-musicians, in areas such as planum temporale, anterior corpus callosum, hand primary motor cortex, anterior-medial Heschl's gyrus, and anterior cerebellum (see Gaser & Schlaug, 2003; Munte, Altenmuller, & Jancke, 2002; Schneider et al., 2002).

Musicians performing rhythmic, sequential finger tapping tasks have been studied with functional neuroimaging. When performing a novel, simple unimanual tapping task, a within-session increase in neural activity in primary motor cortex was detected in musicians, but not in non-musicians, implicating adaptive motor skill processes already acquired or present in musicians (Hund-Georgiadis & von Cramon, 1999). The musicians exhibited at the same time a smaller extent of activation in supplementary motor area (SMA), pre-SMA, and motor cingulate than did non-musicians, implying more efficient motor control processes. Similar activation patterns were observed when musicians perform complex bimanual tapping tasks (Jäncke, Shah, & Peters, 2000), with the exception that less activity is seen in primary motor cortex for musicians than non-musicians. An fMRI study of complex sequences of unimanual finger tapping reported significantly reduced activation for musicians as compared to non-musicians in primary motor and premotor cortices, SMA, and superior parietal cortex (Krings et al., 2000). A metanalysis of neuroimaging studies examined the temporal and sequence ordering involved in the foregoing kinds of tapping tasks (Janata & Grafton, 2003). The results suggested that such tasks elicit responses in sensorimotor cortex, SMA, cerebellum, and premotor cortex. Moreover, with increasing task complexity, other areas appear to be recruited in anterior cingulate, insula, precuneus, intraparietal sulcus, basal ganglia, ventrolateral cortex, and thalamus.

A recent study of attentional states elicited by musical performance suggest that with the use of EEG-based feedback training, musicians can improve the musical quality of their performances (Egner & Gruzelier, 2003). In training sessions prior to musical performance, pianists learned to increase the theta over alpha band amplitudes in their EEG. The enhancements in quality of musical performance appear to be a consequence of a deep relaxed focus of attention, and may not be due to mere reductions in anxiety, as other methods of relaxation training reduced anxiety but did not affect the quality of musical performance.

The brain basis of musical performance per se has been studied in the context of singing or piano playing. One PET investigation studied non-musicians singing simple monotone sequences using a vowel (Perry et al., 1999) and a second fMRI study examined non-musicians overtly or covertly singing a familiar melody without words (Riecker, Ackermann, Wildergruber, Dogil, & Grodd, 2000). A more recent investigation employed PET to examine amateur musicians who performed 'listen and respond' tasks in which they either sang back repetitions of novel melodies, sang back harmonizations to accompany novel melodies, or vocalized monotonically in response (Brown, Parsons, Martinez, Hodges, & Fox, in press). Across these three studies, major singing-specific activations were observed in primary and secondary auditory cortices, primary motor cortex, frontal operculum, SMA, insula, posterior cerebellum, and basal ganglia. However, in the last study, melody singing and harmonization, but not monotonic vocalization, activated planum polare (Brodmann area (BA) 38), implicating it as an area supporting higher musical representations.

In an early, concerted effort to study the brain basis of musical performance (Sergent et al., 1992), pianists were scanned with PET as they performed several conditions involving listening to scales, playing scales, sight-reading a score, and sight-reading a score while playing it. The pianists always heard the sounds they produced on the piano, and they sight-read or played an obscure partita by J.S. Bach. When the pianists played this piece, they used only their right hand. As control conditions, the researchers included a task requiring a manual response to indicate the location of a series of single visual dots within quadrants on a screen and a task with fixation point rest. Of most interest at present is the pattern of activations detected for sight-reading when playing (and hearing) the partita, as contrasted with a combination of the sight-reading and listening conditions. This analysis revealed increases in left frontal operculum (BA 44) that were interpreted to support the patterning of motor sequences of the right hand. There was also activity in left parietal cortex (supramarginal gyrus, BA 40), possibly involved in mapping visual and auditory representations of the melody. There were activations in left occipitoparietal sulcus and bilateral superior parietal cortices (BA 7), which might subserve sensorimotor transformations required for visually guided finger positioning.

Aspects of this early research have been pursued further in a recent study that used fMRI to compare the right hand performance while sightreading the score of a Bartok piano piece to its imagined simulation (Meister et al., 2004). In the baseline control the pianists read score with a single note repeated. Comparing the actual performance to control, the authors observed activations in primarily left sensorimotor areas (BA 2–4), left SMA (BA 6), bilateral precuneus (BA 7), bilateral inferior parietal (BA 40), left occipital (BA 37), left BA 5 (parietal), left posterior cerebellum (VI), midline anterior cerebellum (V), and left thalamus. Several of these activations confirm those in the early PET study (Sergent et al., 1992). Comparing the imagined simulation to control, they observed bilateral superior premotor (BA 6), left frontal (BA 9), bilateral parietal (BA 40 and 7), bilateral occipital (BA 18 and 19), and left posterior cerebellum (VI). A direct comparison between performed and imagined performance revealed performance-specific activations in left sensorimotor (BA 4, 2 and 3), left SMA (BA 6), bilateral inferior parietal (BA 40), right anterior cerebellum (III), and left posterior cerebellum (VI). Activation specific to imagined performance was limited to left occipital (BA 19). These findings are in accord with prior research, such as that by Jeannerod (1994, 1997), which demonstrated that motor and sensory imagery involves psychological and neural processes similar to those for real motor and sensory experiences (on auditory and musical imagery, see Halpern & Zatorre, 1999; Janata, 2001; Reiser, 1992).

Imagined musical performance was also examined in another recent study (Langheim, Callicott, Mattay, Duyn, & Weinberger, 2002). This study combined fMRI data from imagined performance for different instruments (cello, violin, piano) and different memorized compositions (various Vivaldi or Bach pieces) in order to localize common, music-specific areas. Overall, the imagined musical performance (compared to rest) engaged right SMA, right superior premotor cortex (BA 6), right superior parietal lobule (BA 7), right inferior frontal gyrus (BA 47/45), left thalamus, left basal ganglia (caudate), and bilateral posterior cerebellum (VI). This hemodynamic pattern was distinct from that for passive listening to musical pieces and for a self-paced bimanual, finger-tapping task (both compared to rest). Thus, the results were taken to suggest that the foregoing areas are involved in representing information for performing music. It is notable that neither of the two studies just described of imagined musical performance observed activations in temporal cortical regions that support auditory and musical information.

In sum, apart from brain areas for sensory-motor, attention, and executive control processes, three brain regions have been identified so far that appear to be important for higher-level information processing aspects of music performance. One area is the frontal operculum, which can be activated (left, right, or bilaterally) by sight-read piano performance, by music singing, and by imagined string and piano performance of memorized music. This area is often interpreted to be involved in sequence production and imitation learning. A second area is the planum polare, which can be activated (either right or bilaterally) by singing and by sight-read piano performance, but not apparently by imagined musical singing or imagined string or piano playing. This area appears to represent musical representations of a higher order than, for example, is present in more posterior superior temporal cortices (BA 22). A third region of interest in higher-level music is in rostromedial prefrontal cortex, which responds to dissonance and consonance, and to changes in tonality (Blood, Zatorre, Bermudes, & Evans, 1999; Janata et al., 2002; Peretz, Blood, Penhune, & Zatorre, 2001); however, this area has not yet been studied in the context of musical performance.

The goal of the present study was to focus directly on musical performance as such, in order to complement and clarify the foregoing findings. PET was employed to delineate brain areas subserving bimanual piano performance of memorized music. This provides new information relative to prior studies since by recording brain activity when both hands were equally and concurrently producing music, we examined neural systems when both cerebral hemispheres were fully involved in a performance of a natural kind for musicians. This approach goes beyond the Sergent et al. (1992) and Meister et al. (2004) studies in which only the right hand was used to perform the music, a design that left unclear which particular right hemispheric areas may be involved in music performance as such.

In addition, by asking pianists to perform a memorized composition, our design eliminated musical score reading from scanned task performance. In this respect, we examined brain activation during a more purely musical performance. Sight-reading a score during performance adds a considerable cognitive load, one unrelated directly to music performance and cognition per se. Indeed, there is a common belief amongst musicians that a fully memorized piece, one performed without score reading, engenders a distinctly deeper understanding of the composition and more satisfying realization of the piece in performance (Aiello, 2001; Chaffin & Imreh, 2002; Chaffin, Imreh, & Crawford, 2002; Mach, 1998). This belief is congruent with a significant role of a deep focus of attention in the quality of musical performance, as discussed earlier.

Our design referenced the brain activity during the piano performance of a musical composition by J.S. Bach to that during the two-handed performance of scales. The Bach and scales performances required movements of approximately comparable frequency and complexity from each hand. This is a more comparable control contrast than in the Langheim et al. (2002) study for (imagined) memorized musical performance. In this design, real perceived musical sounds and similar executed motor behavior are compared across tasks of varying musical structure to isolate the neural substrates of musical performance. In the Langheim et al. study, imagined sounds and movements were compared to real ones, and the imagined motor behaviors were very different than the control motor behavior (e.g., playing a cello piece versus finger tapping). Nonetheless, it was recognized that studying a natural kind of musical performance, as compared to scales, entailed a number of factors varying to influence brain activity, apart for musicality. Thus, there were intrinsic differences in fingering complexity, independence of hands and melodic lines, complexity of memorized information to recall, emotional content, and attentional demands. The outline of interactions observed here amongst these factors sets the stage for more detailed, parametrically controlled studies of high-level performance skills.

2. Methods

2.1. Participants

After giving informed consent, eight professional musicians (five females and three males) volunteered to participate in this study. All volunteers were right handed (Oldfield, 1971) and ranged from 27 to 54 years of age. Each individual had from 14 to 20 years of training in piano performance, in addition to 10–18 years of training and education on other instruments (either horn, voice, or string) and on other aspects of music (composition and education).

2.2. Stimuli and tasks

Prior to the scanning session, the pianists practiced outside the laboratory in order to attain high quality on each performance to be played from memory in the PET study: the third movement of the Italian Concerto in F Major (BMV 971) by J.S. Bach, and two-handed, two-octave ascending and descending major scales beginning in F major and progressing chromatically upward (e.g., F# major, then G major, etc.). The beginning of each performance is illustrated in Fig. 1. The process of memorizing this movement of the Bach piece has been the object of close psychological study (Chaffin & Imreh, 2002; Chaffin et al., 2002).

During the PET scanning session, subjects performed on a full-sized electronic piano (Yamaha P-132, http://www.yamaha.com) that was mounted above their abdomen (Fig. 2) and adjusted to be comfortable for playing the piano, while minimizing body and head movement. The electronic piano-like sounds produced by the pianists were audible via the built-in speakers in the piano. In all conditions, the subjects' eyes were closed and covered (not shown). The Bach composition was performed from memory, and the scales were executed synchronously (from memory) with both hands at a pace approximating that of the Bach performance. In the rest condition, the subjects lay without movement or auditory stimulation. On a separate day prior to the PET scans, each pianist was given a 1 h practice session playing the Bach composition and scales on the electronic piano while lying supine in the scanner.

2.3. Procedure

The subjects completed each of three tasks (Bach, scales, rest) three times while being scanned. The three tasks were conducted in pseudo-random order, such that PET scan trials 1 through 3 involved a trial (task) of each kind, as did trials
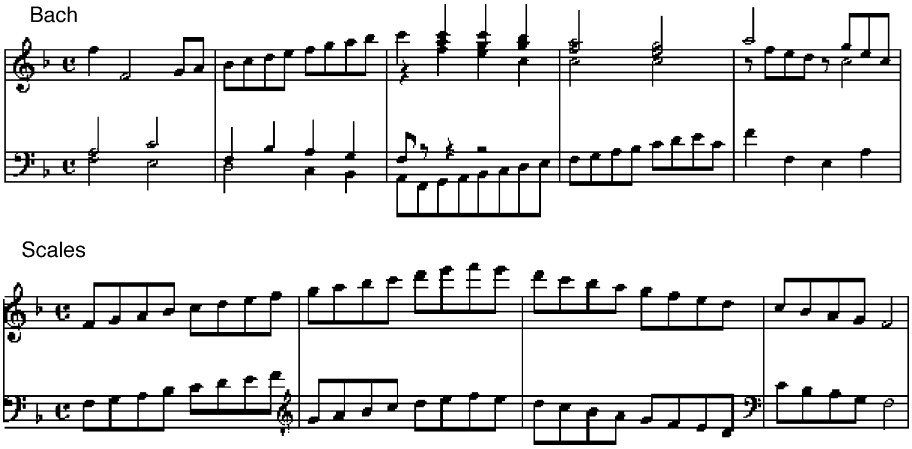
Fig. 1. Shown are the opening sections of stimuli for each performance task. The upper score shows the first four measures of the third movement of the Bach Italian Concerto, and the lower score shows the two-octave F major scale with hands in parallel motion. Note both the similarity of the scalar patterns in the Bach to the scales below, and the comparative independence of the hands in the Bach. There are 68 finger strokes in the concerto, 52 of which are not simultaneous, and 58 in the scales.

Fig. 2. A pianist, viewed from above, lying in the PET scanner, as in the study. (photograph by Stephan Elleringmann (laif photo agency)).

4 through 6, and trials 7 through 9. Within each set of three trials, the order was completely random.

During the PET session, subjects lay supine in the scanning instrument, with the head immobilized by a closely fitted thermal-plastic facial mask with openings for the eyes, ears, nose, and mouth. The subjects began performing the Bach composition or scales 30 s prior to injection of the bolus. The ^{15}0-water bolus uptake required approximately 20 s to reach the brain at which time a 40 s scan was triggered by a sufficient rate of coincidence-counts, as measured by the PET camera. At the end of the 40 s scan, the experimenter verbally interrupted the performance to terminate the task, immediately after which the subject lay quietly without moving during a second scan (50 s). From the initiation of the task until the start of the second scan on each trial, each pianist played approximately 2 min. On trials with the Bach concerto, the pianists began at the beginning of the third movement; on trials with scales, they began with F major.

The PET scans were performed on a GE 4096 camera, with a pixel spacing of 2.0 mm, and inter-plane, center-to-center distance of 6.5 mm, 15 scan planes, and a *z*-axis field of view of 10 cm. Images were reconstructed using a Hann filter, resulting in images with a spatial resolution of approximately 7 mm (full-width at half-maximum). The data were smoothed with an isotropic 10 mm Gaussian kernel to yield a final image resolution of approximately 12 mm. Anatomical MRI scans were acquired on an Elscint 1.9 T Prestige system with an in-plane resolution of 1 mm^2 and 1.5 mm slice thickness. The PET field of view was adjusted per subject such that when the group mean functional PET blood flow image was spatially normalized, co-registered and superimposed on anatomical MRI, activation was detectable at full axial plane for *z* height of 56 mm (see illustration in center of Fig. 3).

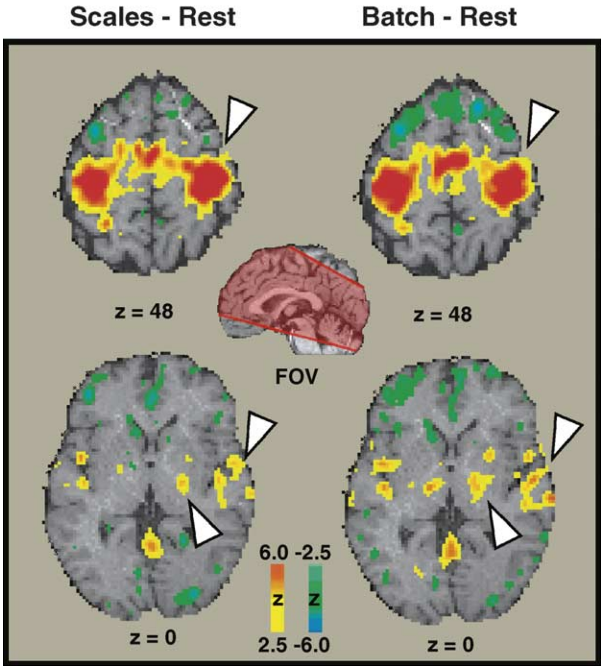

Fig. 3. Significant blood flow changes as pianists play scales, and as pianists play the Bach composition. Arrows on the upper images point to sensorimotor areas; arrows on the lower images point to auditory temporal cortex and thalamus. Shown are group-averaged PET images, contrasted with rest, and overlaid onto a single representative subject's anatomical MRI. PET data are *z*-scores displayed on a color scale ranging from 2.58 (yellow; $P < 0.01$) to 6.0 (red; $P < 0.0001$) for activations and −2.58 (green, $P < 0.01$) to −6.0 (blue; $P < 0.0001$) for deactivations. Throughout, the *z*-values indicate the axial height of the brain volume relative to Talairach and Tournoux (1988) stereotactic coordinates, and the left sides of the brain images are the left side of the brain. The effective field of view for group mean functional PET data is illustrated by the central image.

Imaging procedures and data analysis were performed exactly as described in Parsons and Osherson (2001), adhering to methods described in Raichle, Martin, Herskovitch, Mintun, and Markham (1983), Fox, Mintun, Reiman, and Raichle (1988), and Mintun, Fox, and Raichle (1989). Briefly, local extrema were identified within each image with a 3D search algorithm (Mintun et al., 1989) using a 125 voxel search cube (2 mm^3 voxel). A beta-2 statistic measuring kurtosis and a beta-1 statistic measuring skewness of the extrema histogram (Fox & Mintun, 1989) were used as omnibus tests to assess overall significance (D'Agostino, Belatner, & D'Agostino, 1990). Critical values for beta statistics were chosen at $P < 0.01$. If the null hypothesis of omnibus significance was rejected, then a post hoc (regional) test was done (Fox & Mintun, 1989; Fox et al., 1988). In this algorithm, the pooled variance of all brain voxels is used as the reference for computing significance. This method is distinct from methods that compute the variance at each voxel but is more sensitive in that results are more reproducible across sample sizes of 1–8 (Strother et al., 1997), particularly for small samples, than the voxel-wise variance methods of Friston, Frith, Liddle, and Frackowiak (1991) and others. The critical-value threshold for regional effects ($z > 2.58$, $P < 0.005$, one-tailed) is not raised to correct for multiple comparisons since omnibus statistics are established before post hoc analysis.

Gross anatomical labels were applied to the detected local maxima using a volume-occupancy-based, anatomical labeling strategy as implemented in the Talaraich Daemon^{TM} (Lancaster et al., 2000), except for activations in the cerebellum which were labeled with reference to an atlas of the cerebellum (Schmahmann et al., 1999).

3. Results

The performance of scales, when contrasted with rest, activated an array of motor, somatosensory, and auditory functional areas, among others (Table 1 and Fig. 3). Responses were observed in bilateral primary motor cortex for hand (BA 4), left SMA, bilateral predominantly left insula (BA 13), bilateral dorsolateral premotor cortex (BA 6), right motor cingulate, right pulvinar, left lateral globus pallidus, and right red nucleus. There were also increases in bilateral superior temporal gyrus (BA 22), right inferior temporal cortex (BA

Table 1
Scales–rest

Coordinates			Region (Brodmann area)	*z*-Score	Extent (mm^3)
x	*y*	*z*			
Activations					
−34	−22	54	Precentral gyrus (BA 4)	10.66	1000
40	−24	50	Postcentral gyrus (BA 3)	9.96	1000
34	−22	48	Precentral gyrus (BA 4)	9.91	744
2	−6	46	Cingulate gyrus (BA 24)	6.83	968
−6	−4	50	Medial frontal gyrus (SMA, BA 6)	5.72	872
−44	0	−2	Insula	5.30	648
16	−16	52	Medial frontal gyrus (BA 4)	5.20	984
−44	−17	4	Insula (BA 13)	5.11	696
52	−4	−4	Superior temporal gyrus (BA 22)	5.11	792
−18	−2	48	Medial frontal gyrus (BA 6)	4.64	832
−9	−28	40	Cingulate gyrus (BA 31)	4.60	560
56	−10	4	Superior temporal gyrus (BA 22)	4.50	648
18	−24	8	Thalamus (pulvinar)	4.41	448
44	−14	−1	Insula (BA 13)	4.18	528
−16	36	12	Anterior cingulate (BA 32)	4.13	264
8	−22	46	Paracentral lobule (BA 24)	4.09	704
51	0	30	Precentral gyrus (BA 6)	3.71	488
−20	−8	2	Lateral globus pallidus	3.71	264
42	−34	18	Superior temporal gyrus (BA 41)	3.67	416
52	−24	22	Inferior parietal lobule (BA 40)	3.62	480
46	−22	2	Superior temporal gyrus (BA 22)	3.53	496
−46	−32	20	Insula	3.43	416
5	−24	−4	Red nucleus	3.29	280
−42	0	12	Insula (BA 13)	3.15	192
52	−54	−12	Inferior temporal gyrus (BA 20)	3.11	144
Anterior cerebellum activations					
12	−54	−14	Culmen (V)	11.49	1000
22	−54	−22	Culmen (V)	11.21	1000
0	−60	−12	Culmen (V) (Vermis)	10.61	1000
−12	−52	−20	Culmen (IV)	10.33	1000
2	−38	−16	Central lobule (III)	4.32	536

Table 2
Bach–rest

Coordinates			Region (Brodmann area)	*z*-Score	Extent (mm^3)
x	*y*	*z*			
Activations					
−32	−24	50	Precentral gyrus (BA 4)	11.95	1000
40	−24	52	Precentral gyrus (BA 4)	11.49	1000
6	−4	52	Medial frontal gyrus (BA 6)	7.80	1000
−6	−12	50	Medial frontal gyrus (BA 6)	6.97	992
−44	−2	−4	Insula (BA 13)	5.77	984
54	−12	2	Superior temporal gyrus (BA 22)	5.26	856
−42	−16	2	Insula (BA 13)	5.17	712
48	−30	4	Superior temporal gyrus (BA 22)	4.98	784
−14	−18	2	Thalamus (mammillary body)	4.89	696
52	0	−6	Superior temporal gyrus (BA 38)	4.66	880
16	−26	6	Thalamus (pulvinar)	4.52	592
26	4	−2	Lentiform nucleus (putamen)	4.29	504
16	−16	0	Thalamus	4.15	800
16	−10	0	Red nucleus	4.06	344
−18	0	48	Medial frontal gyrus (BA 6)	3.88	768
36	−2	18	Insula	3.88	456
6	−34	−10	Midbrain	3.88	472
−40	−2	12	Insula	3.79	248
4	−24	48	Paracentral lobule (BA 31)	3.74	512
32	−56	−9	Fusiform gyrus	3.69	304
50	−24	18	Insula	3.56	448
48	−44	−10	Inferior temporal gyrus (BA 37)	3.51	104
−24	−14	4	Lentiform nucleus (globus pallidus)	3.46	272
−40	−26	8	Superior temporal gyrus (BA 22/42)	3.32	432
8	4	35	Cingulate gyrus (BA 24)	3.28	312
−28	−2	4	Lentiform nucleus (putamen)	3.28	416
Anterior cerebellum activations					
14	−56	−14	Culmen (V)	14.07	1000
0	−62	−14	Culmen (V)	12.78	1000
−10	−56	−18	Culmen (V)	10.80	1000
−18	−54	−18	Culmen (V)	10.47	840
Posterior cerebellum activations					
0	−66	−26	Declive (VI) (vermis)	11.30	1000
−12	−70	−30	Dentate nucleus	6.32	896
28	−73	−16	Quadrangular (VI)	3.79	376

20), bilateral anterior cingulate (BA 32 and 31), and right inferior parietal cortex (BA 40). In anterior cerebellum, there was activity in culmen (V, IV) in bilateral intermediate and midline (vermal) regions, and in the central lobule (III).

Playing the Bach concerto, when contrasted with rest, likewise revealed a distributed pattern of activations in motor, somatosensory, auditory, and other structures (Table 2 and Fig. 3). Responses were observed in bilateral primary motor cortex for hand (BA 4), bilateral SMA, bilateral insula (BA 13), left dorsolateral premotor cortex (BA 6), and right red nucleus. There was also strong subcortical activity in bilateral thalamus (left mammillary body, right pulvinar) and bilateral basal ganglia (left globus pallidus, bilateral putamen). There were strong responses in bilateral, predominantly right superior temporal cortex (BA 22), and right planum polare (BA 38). Other activated areas included right cingulate gyrus (BA 24) and right occipitotemporal cortex (BA 37). In anterior cerebellum, there was bilateral activity in intermediate and midline (vermal) regions of culmen (V). In posterior cerebellum, there were responses in declive of vermis, right quadrangular lobule (VI), and left dentate nucleus.

In the direct contrast between the performance of the Bach composition and scales, there were a variety of activations specific to the Bach (Table 3). There were strong responses in subcortical areas, including bilateral, predominantly right, thalamus, and bilateral basal ganglia (bilateral lentiform nucleus and left caudate nucleus). There were activations in somatomotor-related regions, including bilateral dorsolateral premotor cortex (BA 6), bilateral primary motor cortex (BA 4), right insula, and right SMA. There were strong increases detected in bilateral superior temporal gyrus (BA 22) and planum polare (BA 38), as well as activity in bilateral lingual gyrus (BA 19 and 18) and bilateral posterior cingulate (BA 31 and 23). Increases were detected in posterior cerebellum (declive of vermis (VI) and quadrangular lobule (VI)), as well as in anterior cerebellum (left culmen (IV)).

Table 3
Bach–scales

Coordinates			Region (Brodmann area)	z-Score	Extent (mm^3)
x	*y*	*z*			
Activations					
11	−18	16	Thalamus	4.29	656
16	−34	6	Thalamus	4.25	608
28	−76	−4	Lingual gyrus (BA 19)	4.25	680
36	−2	18	Insula	4.16	624
48	2	2	Superior temporal gyrus (BA 22)	3.52	424
−4	−73	0	Lingual gyrus (BA 19)	3.52	440
7	−30	−16	Midbrain	3.52	608
6	−6	52	Medial frontal gyrus (BA 6, SMA)	3.43	592
26	−62	12	Posterior cingulate (BA 31)	3.43	416
−49	−8	2	Superior temporal gyrus (BA 22)	3.43	488
26	6	−4	Lentiform nucleus	3.43	672
−40	−10	38	Precentral gyrus (BA 4)	3.34	552
−13	14	10	Caudate	3.29	464
−26	−4	8	Lentiform nucleus	3.25	616
−20	−30	38	Cingulate gyrus (BA 31)	3.16	264
−50	−4	28	Precentral gyrus (BA 6)	3.16	728
−2	−78	18	Cuneus (BA 18)	3.16	344
−10	−32	6	Thalamus	3.16	320
38	−12	30	Lateral sulcus, precentral G. (BA 6)	3.11	320
−42	−14	28	Lateral sulcus, precentral G. (BA 6)	3.11	560
−4	−40	22	Posterior cingulate (BA 23)	3.11	272
−21	−70	−2	Lingual gyrus (BA 18)	3.11	592
Anterior cerebellum activations					
16	−58	−14	Culmen (V)	4.57	960
−8	−64	−8	Culmen (V)	4.43	768
18	−50	−14	Culmen (V)	4.16	792
−7	−46	−16	Culmen (IV)	3.52	640
Posterior cerebellum activations					
−2	−66	−26	Declive (vermis) (VI)	4.25	760
38	−52	−20	Quadrangular lobule (VI)	3.93	576
−9	−73	−16	Quadrangular lobule (VI)	3.66	464
−13	−72	−31	Quadrangular lobule (VI)	3.61	384
16	−84	−16	Quadrangular lobule (VI)	3.48	288
26	−62	−23	Quadrangular lobule (VI)	3.34	464
−22	−75	−18	Quadrangular lobule (VI)	3.25	344
8	−62	−22	Quadrangular lobule (VI)	3.16	576

In the direct contrast between the performance of scales and the concerto, there were numerous increases specific to scales (Table 4). Strong activations were seen in bilateral anterior cingulate gyrus (BA 31 and 32), bilateral middle temporal cortex (BA 21), and right superior temporal cortex (BA 41). There were responses in right frontal regions (BA 9 and 10), right temporoparietal regions (BA 39 and 40), right fusiform gyrus (BA 37), left inferior frontal gyrus (BA 47), right precuneus (BA 7), and right primary motor cortex (BA 4). Increases were also detected in anterior and posterior cerebellum (culmen (IV) and quadrangular lobule (VI), respectively).

To visualize the increases in the two performances (Fig. 4), each voxel was characterized as responding for the Bach only, for the scales only, or for both. Areas responding in common for playing Bach and scales included motor and somatosensory cortices and SMA (Fig. 3 upper left and right), as well as superior and middle anterior temporal cortex, preferentially on the right (Fig. 4), and anterior cerebellum (Fig. 4, bottom row). Other activations (not shown) included bilateral inferior parietal cortex (BA 40), bilateral SMA (BA 6), bilateral motor cingulate (BA 24), right thalamus, bilateral anterior cerebellum (III–V), and bilateral posterior cerebellum (VI, vermus).

Compared to playing scales, the performance of the concerto more strongly activated the superior, middle, and inferior temporal lobe, particularly on the right side, as well as thalamus (Fig. 4, lower left). Playing Bach more strongly activated left dorsolateral premotor cortex (BA 6, Fig. 4, upper left), whereas playing scales activated a corresponding area in right dorsolateral premotor cortex, but to a lesser extent (Fig. 3, upper left). Other activations (not shown, see Table 3) included bilateral basal ganglia, bilateral dorsolateral premotor, bilateral primary motor, right insula, right SMA, bilateral lingual and cuneous regions, posterior cingulate, and anterior and posterior cerebellum.

Table 4
Scales–Bach

Coordinates			Region (Brodmann area)	z-Score	Extent (mm^3)
x	*y*	*z*			
Activations					
0	−56	30	Cingulate gyrus (BA 31)	−4.17	920
−2	−56	28	Cingulate gyrus (BA 31)	−4.17	208
−50	−29	−7	Middle temporal gyrus (BA 21)	−3.85	648
0	32	34	Cingulate (BA 32)	−3.80	608
2	−44	32	Cingulate gyrus (BA 31)	−3.53	744
57	−16	−10	Middle temporal gyrus (BA 21)	−3.53	656
32	14	36	Middle frontal gyrus (BA 9)	−3.49	744
4	−48	20	Posterior cingulate (BA 30)	−3.49	608
42	−35	16	Superior temporal gyrus (BA 41)	−3.44	344
4	−56	38	Precuneus (BA 7)	−3.39	680
−48	20	2	Inferior frontal gyrus (BA 47)	−3.30	216
46	−56	−12	Fusiform gyrus (BA 37)	−3.30	432
−40	−64	26	Middle temporal gyrus (BA 39)	−3.26	456
48	−52	30	Supramarginal gyrus (BA 40)	−3.17	536
44	−64	30	Middle temporal gyrus (BA 39)	−3.17	688
50	−6	32	Precentral gyrus (BA 4)	−3.12	648
14	46	22	Medial frontal gyrus (BA 10)	−3.12	504
Anterior cerebellum activations					
20	−32	−14	Culmen (IV)	−4.35	648
Posterior cerebellum activations					
35	−63	−24	Quadrangular lobule (VI)	−3.49	296

Scales performance activated certain middle temporal areas that were not activated by playing Bach (Fig. 4, upper right). Other activations (not shown, see Table 4) specific to playing scales included posterior cingulate cortex, right middle frontal gyrus (BA 9), right precuneus (BA 7), left inferior frontal gyrus, right temporoparietal areas, right fusiform gyrus, right precuneus gyrus, and right prefrontal cortex (BA 10).

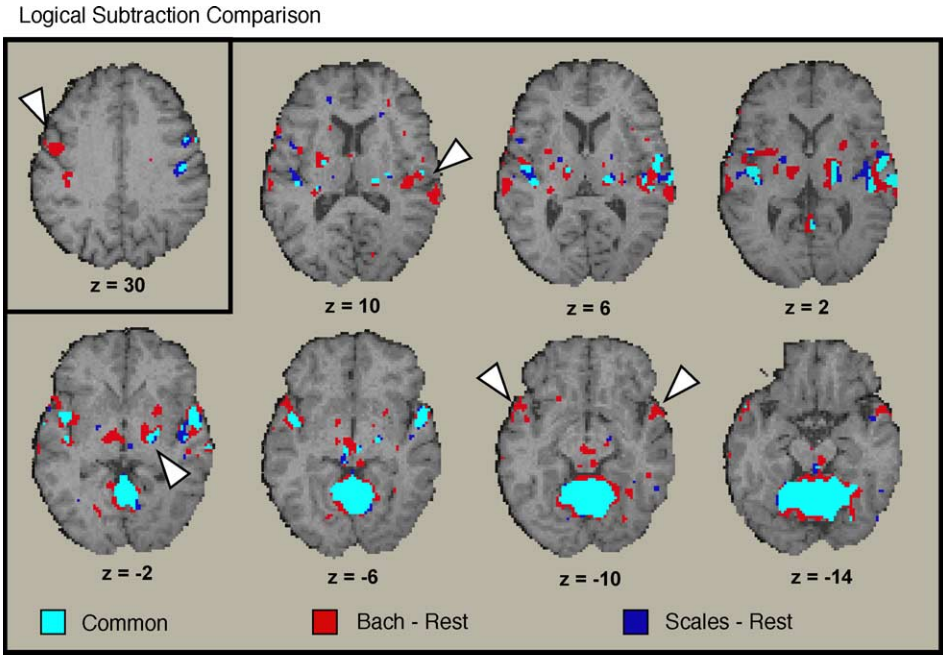

Fig. 4. Examples of the significant blood flow activations specific to the performance of the Bach composition (red), specific to the performance of scales (blue), and common to both performances (cyan). Arrows highlight some areas with greater activation for performance of Bach composition. Note, for example, in the upper image, that Bach activates left premotor cortex (BA 6), whereas scales activates a corresponding area on the right. Also highlighted are greater activations specifically during the Bach performance in thalamus and basal ganglia and in bilateral temporal pole (including planum polare, BA 38). Shown are logical contrasts of Bach vs. rest and scales vs. rest, in group-averaged PET images overlaid on anatomical MRIs.

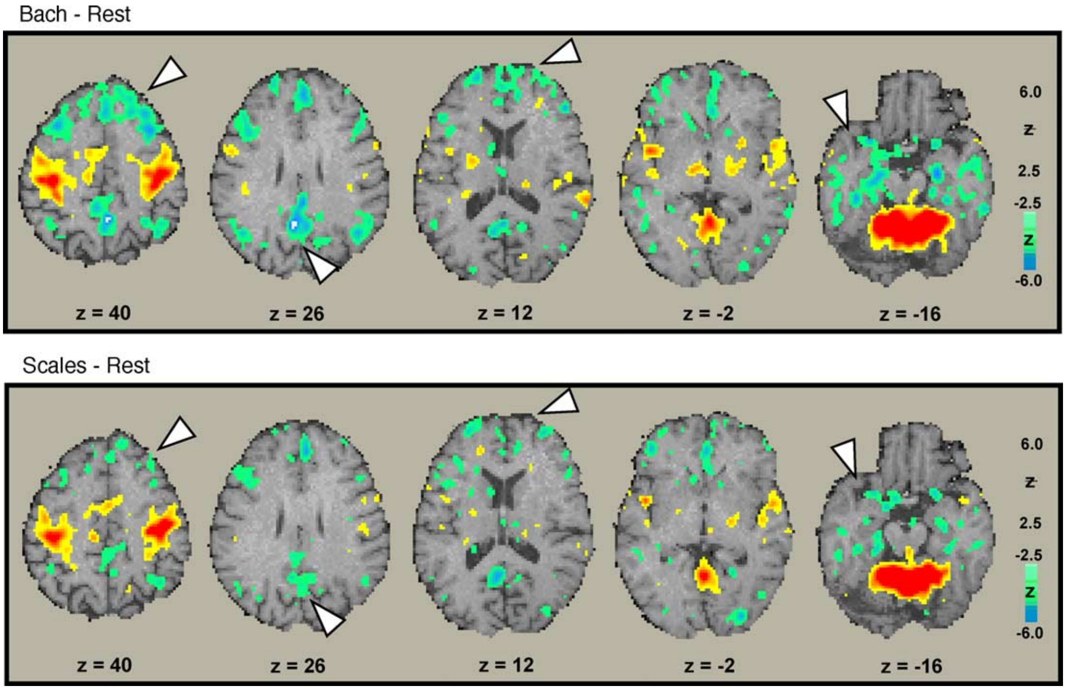

Fig. 5. Examples of the more intense and extensive blood flow decreases (in green–blue color) when pianists play the Bach composition (upper row) as compared to scales (lower row). Image volumes shown here range from $z = 40$ mm down to -16 mm, in 14 mm increments; the corresponding $z = 48$ mm volumes are shown in upper images in Fig. 2. Shown are group-averaged PET images, contrasted with rest, and overlaid onto a single representative subject's anatomical MRI. PET data are z-scores displayed on a color scale ranging from -2.58 (green, $P < 0.01$) to -6.0 (blue; $P < 0.0001$) for deactivations, and 2.58 (yellow; $P < 0.01$) to 6.0 (red; $P < 0.0001$) for activations.

There was an unexpected intensity and extent of deactivation during the performance of Bach, more than was present during the scales performance (Fig. 5). In a conjoint measure of deactivation intensity and extent (relative to rest), there was 43% greater deactivation throughout the brain during the Bach performance than scales. The deactivated areas for the Bach performance included frontal areas (BA 8, 9 and 44), posterior cingulate areas (BA 31), bilateral middle temporal, parahippocampus, precuneus, and posterior cerebellum. Some of those regions were deactivated for the scales performance, but to a lesser extent.

4. Discussion

These data offer an initial glimpse of brain areas engaged when an expert pianist plays a memorized musical composition. Psychological study of the process of memorizing the composition performed in this study has characterized the nature of the extensive preparation for performance, particularly the role of conceptual, auditory, and motor memory processes (Chaffin & Imreh, 2002; Chaffin et al., 2002). Our discussion first considers the functional brain data common to the performance of scales and the music composition, then considers the data specific to performing musical compositions, and concludes with commentary on the functional data specific to the generation and performance of scales.

The brain regions engaged for playing and hearing tones on the piano per se, independent to a degree of the kind of musical structure being played, are outlined in the activations in common for the performances of scales and the Bach concerto. On this analysis, there is a distributed network of areas including bilateral primary motor cortex for hand and arm (BA 4), corresponding somatosensory areas (BA 3, 1 and 2), bilateral inferior parietal cortex (BA 40), bilateral SMA (BA 6), bilateral motor cingulate (BA 24), bilateral superior and middle temporal cortex (BA 22, 21, and 38 (planum polare)), right thalamus, bilateral anterior cerebellum (III–V), and bilateral posterior cerebellum (VI, vermus).

Published research suggests pertinent functions that may underlie playing and hearing tones on the piano as such. Motor sensory areas were engaged by requirements for finger and arm movement in bimanual piano performance. These regions are known to be involved in the execution of planned motor output (e.g., Carpenter, Georgopoulos, & Pellizzer, 1999; Graziano, Taylor, Moore, & Cooke, 2002; Zilles et al., 1995). SMA is likely involved in memory and sequencing of self-generated, internally guided composite movements. Motor cingulate has recently been observed to be active during bimanual tapping tasks for in-phase, but not for anti-phase or polyrhythmic, coordination (Ullen, Forssberg, & Ehrsson, 2003), consistent with its activation here for the in-phase coordination required in these tasks. The thalamus may be involved in linking sensory and motor parameters (Connors, Landisman, & Reid, 1998; Guillery, 2003), in the present case, for the execution of fine coordination of keyboard fingering and tone production. The anterior cerebellum is likely supporting sensory processing associated with arm and finger movements (Bower & Parsons, 2003; Liu et al., 2000; Parsons & Fox, 1997). The activated posterior cerebellar areas have been implicated in discrimination tasks involving pitch and melody (Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003; Griffiths, Johnsrude, Dean, & Green, 1999; Holcomb et al., 1998; Parsons, 2003). The inferior parietal areas activated in this analysis may support multi-modal associations (tactile, motor, auditory), which are important to action planning and execution in this context (Duhamel, Colby, & Goldberg, 1998; Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997; Milner & Goodale, 1995; Sakata, 1996).

Also implicated in these components of performance were bilateral superior and middle temporal cortex, wherein reside areas implicated in various music perception tasks, as described in Section 1 and later. Note that in the Sergent (1993) study, the peak activation in this region for the condition of passively listening to scales (minus visual fixation) was −56, −4, 2, which is homologous to the right hemispheric ones here (52, −4, −4, and 56, −10, 4) for playing and hearing scales (i.e., blindfolded and contrasted with eyes closed rest). This suggests a hemispheric difference depending on the presence of an action–perception cycle like that when playing bimanually, but not merely listening to, memorized scales.

There were a variety of hemodynamic changes specifically related to the performance of the Bach concerto. Strong increases were evident in secondary auditory association areas, including bilateral superior and middle temporal cortex and planum polare. Very active areas appeared as well in bilateral thalamus, bilateral basal ganglia, and posterior cerebellum. Increases in motor-sensory areas were detected in bilateral dorsolateral premotor, bilateral primary motor, right insula, right SMA, and anterior cerebellum. There were increases in bilateral lingual regions and posterior cingulate. Each of these areas has been linked by data and hypotheses to specific functions that could conceivably play a direct or indirect role in skilled piano playing of memorized pieces.

The foregoing activated superior and middle temporal areas (BA 22 and 21) have been implicated in a variety of music perception tasks, including tone and melody processing (Zatorre, 2003). These regions also appear to process harmony, as when expert musicians sight-read a novel musical score to detect harmonic errors heard in the performance of the score (Parsons et al., 1998) or when musically experienced listeners track a melody as it changes keys (Janata et al., 2002). In the performance of the memorized concerto, it is likely that these regions subserve the auditory anticipations of the recalled composition, as well as recognition of the produced piano sounds.

The activation of the planum polare for the performance of Bach, but less so for scales, confirms other data implicating this area in representing complex melody and harmony (Brown et al., in press; Griffiths, Buchel, Frackowiak, & Patterson, 1998; Koelsch et al., 2002; Samson & Zatorre, 1988; Warrier & Zatorre, 2004; Zatorre, 1985; Zatorre & Belin, 2001). The concerto performance activated a more extensive region of these areas than did playing scales, often extending in the dorsal–ventral direction. This role of the planum polare appears at current levels of resolution to be independent of features of the musical activities such as whether the music is sung or played on piano (singing and playing music activate overlapping regions), and which of its musical features one is closely attending to. The planum polare, as well as activated areas in superior and middle temporal cortex, likely operate in conjunction with ventral and lateral frontal cortical areas implicated for auditory working memory and monitoring in music tasks (Zatorre, 2003).

The thalamus, also active for music performance, may be involved in linking sensory and motor parameters (Connors et al., 1998; Guillery, 2003), and here may fill such a role in the execution of fine keyboard fingering and precisely timed tone production (with eyes closed). This activation likely reflects the escalating demands, different in kind and quantity from those for scales (i.e., interpretative, expressive, phrasing features of performance), and related to the close coordination of kinesthetic, tactile, motor, auditory, and affect information.

The basal ganglia, also strongly activated, have been associated with selecting and organizing segments of action, including their timing (Houk, Davis, & Beiser, 1995; Jog, Kubota, Connolly, Hillegaart, & Graybiel, 1999; Kermadi & Joseph, 1995; Redgrave, Prescott, & Gurney, 1999). Their activation for playing the concerto is probably in response to specific requirements for the selection and organizing of independent sequences and phrases for each hand and each melodic voice.

The increased activity in right SMA likely reflects increased demand for independent coordination of the left hand during the Bach concerto, as compared to scales. SMA is often associated with memory and sequencing of self-generated, internally guided composite movements (Crammond & Kalaska, 1996; Passingham, 1996; Tanji & Shima, 1994). In playing scales, the non-dominant left hand can be guided by the right hand, but in the concerto the left hand is expected to achieve an autonomous melodic continuity.

Insula, which was activated on the right in the Bach performance, has been associated with higher levels of somatic function (Schneider, Friedman, & Mishkin, 1993), and here could be involved in integrating information from the whole body to support the coordination of bimanual performance. The specific increase beyond that for scales, may be in response to the greater parity required in autonomy of the two sequences of manual actions and melodic lines.

There were also increases in dorsal premotor cortex (e.g., seen in two left hemispheric foci in the upper left image of Fig. 4). This region is often linked to planning, programming, initiation, guidance, and execution of movements (see review by Passingham, 1993), and its activation here would accord with the escalating need for motor planning and programming required for increased control and coordination in the Bach concerto.

Musical performance also specifically activated posterior regions of cerebellum in the vicinity of the primary fissure. Although the weight of the evidence has now shifted in favor of the cerebellum (particularly the posterior hemispheres) performing non-motor functions, there is no consensus as to exactly how to characterize those function(s) (Bower & Parsons, 2003; Ivry & Fiez, 2000; Schmahmann et al., 1999; Vokaer et al., 2002). Indeed, recent neuroimaging studies of pitch or melody discrimination, as dissociated from motor coordination or cerebral motor cortical activity, have implicated regions of posterior cerebellum (V and VI) bilaterally (Gaab et al., 2003; Griffiths et al., 1999; Parsons, 2003) or on the left (Holcomb et al., 1998). Activations observed here specifically for the concerto are in these regions, thus suggesting that the activations are supporting aspects of the perception of melody. Be that as it may, viable alternative candidate functions, pertinent to musical performance, include the monitoring of errors (Fiez, Petersen, Cheney, & Raichle, 1992), executive and attentional control (Akshoomoff, Courchesne, & Townsend, 1997; Hallett & Grafman, 1997), perceptual motor timing and response preparation (Ivry, 1997), control of the acquisition of sensory information (Bower, 1997; Bower & Parsons, 2003), and internal forward-inverse modelling of sensory-motor-spatial aspects of the performance (Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003). The additional activity in anterior cerebellum for the concerto may relate to sensory processing associated with bimanual arm and finger movements (Bower & Parsons, 2003; Liu et al., 2000; Parsons & Fox, 1997) or alternatively to one of the foregoing candidate cerebellar functions.

Regions of posterior cingulate cortex, also activated specifically for musical performance, have been implicated in three functions: episodic memory (Grasby et al., 1993; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Maddock, Garrett, & Buoncore, 2001), mediating interactions between emotional and memory processes (Maddock, Garrett, & Buoncore, 2003), and monitoring stimuli in the environment (Raichle et al., 2001; Vogt, Finch, & Olson, 1992). This region has luxuriant afferent projections from areas associated with emotion and social information such as subgenual anterior cingulate, orbitofrontal, superior temporal, and dorsolateral prefrontal cortices (Allison, Puce, & McCarthy, 2000; Carmichael & Price, 1995; Morris, Pandya, & Petrides, 1999; Vogt & Gabriel, 1993). In addition, the functional data implicating posterior cingulate in memory processing (e.g., Grasby et al., 1993) is corroborated by reciprocal projections with memory structures in medial temporal cortex and with thalamic nuclei (Bentovoglio, Kultas-Ilinsky, & Ilinsky, 1993; Suzuki & Amaral, 1994). In this context, it is conceivable that the role of these activated regions of posterior cingulate could be in mediating and monitoring both the use of the memorized music composition and the unfolding contour of its implied emotive, interpretative, and expressive features.

The activations in cuneus and bilateral lingual cortex, which occurred in spite of pianists being blindfolded, suggest the use of visual imagery. Comparable activations in visual areas have been observed in other neuroimaging studies of music experiences, including both imagined and actual performance (Brown et al., in press; Langheim et al., 2002), as well as imagined and actual listening (Halpern & Zatorre, 1999; Janata et al., 2002; Platel et al., 1997; Satoh, Takeda, Nagata, Hatazawa, & Kuruhara, 2001; Zatorre, Evans, & Meyer, 1994). The activations in visual areas in the present study may result if subjects visualize their own hands playing piano (Jeannerod, 2004) or visualize notes on stave of the score (Bihan et al., 1993; Klein, Paradis, Poline, Kosslyn, & LeBihan, 2000).

The pattern of increases for the musical performance here can be compared to those for right-handed piano performance, singing, and imagined musical performance. As discussed earlier, the Sergent et al. (1992) study of right handed piano performance (contrasted with sight reading and listening) found activations in left frontal operculum, left dorsolateral premotor, left parietal cortex, as well as left occipitoparietal and bilateral superior parietal regions. None of these activated areas, with the exception of the left dorsolateral premotor cortex, responded during the bimanual performance of a memorized composition. These differences between the two studies are very likely related to differences in experimental parameters, including contrast controls, bimanual versus unimanual performance, blindfolded versus visually guided performance, and memorized versus not memorized composition.

In the three neuroimaging studies of singing described earlier (Brown et al., in press; Perry et al., 1999; Riecker et al., 2000), singing-specific activations appeared in primary and secondary auditory cortices, primary motor cortex, frontal operculum, SMA, insula, posterior cerebellum, and basal ganglia. Playing the piano composition activated areas in each of these structures, with the exception of the frontal operculum. Note that frontal operculum was active in the Sergent et al. analysis of playing a sight-read composition, contrasted with sight-reading and listening. Thus, in combination, these studies indicate that activation in frontal operucular areas can be elicited for either production modality (singing or piano playing). Moreover, as noted earlier, musical piano playing, melody singing, and harmonization, all activated overlapping regions of the planum polare, implicating it as a key area for the high level musical representation.

When musicians imagined playing memorized musical compositions (Langheim et al., 2002), there were activations, combining over strings and piano performance and contrasting with rest, in right SMA, right superior premotor cortex, right superior parietal lobule, right frontal operculum, left thalamus, left basal ganglia, and bilateral posterior cerebellum. Playing the Bach concerto activated regions in each of these structures, with exception of the frontal operculum and superior parietal cortex.

Thus, apart from sensory-motor, attention, and executive control processes, the three apparently key regions emerging as important in higher-level aspects of music performance show the following tendencies. The planum polare (BA 38) is activated (either right or bilaterally) by singing and by playing sight-read or memorized music on piano, but is not appreciably activated by imagined musical singing or by imagined string or piano performance of memorized music. The frontal operculum (typically BA 44) is activated (either left, right, or bilaterally) by music singing and by imagined string and piano performance of memorized music, but is not detectably engaged by the performance of memorized piano music. The rostromedial prefrontal cortex, which responds to dissonance and consonance, and to changes in tonality, was not appreciably activated during the Bach performance.

It is notable that areas subserving emotion and reward that are active during musical listening (Blood & Zatorre, 2001; Blood et al., 1999; Brown, Martinez, & Parsons, 2004; Peretz et al., 2001) were not appreciably active during the performance of the concerto, which is associated by pianists with vibrant emotional structure (Chaffin & Imreh, 2002; Chaffin et al., 2002). Indeed, no such activations were reported in other musical performances, whether imagined or actual, that have been studied with neuroimaging (Brown et al., in press; Langheim et al., 2002; Meister et al., 2004; Riecker et al., 2000; Sergent et al., 1992). Additional research is required to clarify this observation.

Surprisingly, there was a great deal of deactivation detected here, particularly during the performance of the Bach concerto, which exhibited nearly fifty percent greater deactivation throughout the brain (compared to rest) than did the scales performance. During performance of the musical composition, deactivation foci were observed in frontal regions (BA 8, 9, and 44), posterior cingulate areas (BA 31), bilateral middle temporal cortex, parahippocampus, precuneus, and posterior cerebellum. These deactivations, apparently in areas not directly relevant to musical performance, may reflect a much deeper focused attention for performing the musical piece than for playing scales.

The deactivations may be a consequence of inhibition of processes potentially able to distract the musician during a sustained performance. This possibility could be consistent with the finding discussed earlier that feedback training to enhance slow-wave EEG improves the quality of musical performances (Egner & Gruzelier, 2003). Likewise, musicians report anecdotally that they “lose themselves” in absorption during peak musical performances (Chaffin & Imreh, 2002; Chaffin et al., 2002; Csikszentimihalyi & Csikszentimihalyi, 1988; Mach, 1998).

Some deactivated processes, perhaps those in executive function, cognitive association, and general memory areas, etc., may be likely to be active during rest, so to some extent their appearance as deactivations in the task state could be an artifact of a subtraction contrast. However, the possibility that the deactivations per se are genuine suspensions of activity is consistent with a recent PET study of the resting state that used oxygen extraction fraction both to begin characterizing brain areas that are active during rest (during an open attentive state) and to document their deactivation or suspension during specific goal directed behaviors (Raichle et al., 2001). These researchers identified areas in precuneus, posterior cingulate, and medial prefrontal cortex that appear to be tonically active, for example, with the precuneus and posterior cingulate continuously collecting information from the environment that can be evaluated for salience with assistance of areas in medial and orbital frontal cortices. As shown in Fig. 5, some of these areas were deactivated here, particularly in the performance of the Bach concerto. While such tonically active circuits may be suspended for any goal-driven activity, deeply attentive states associated with intense musical performance, among other similarly intense activities, may involve the suspension of a wider range of brain processes, as suggested by the overall deactivations seen here.

Briefly then, here is a summary outline of the distributed set of areas and functions implicated by these data specifically for the performance of memorized musical pieces, beyond those common to performing scales and the musical piece. The activations in lingual and cuneus areas reflect subjects’ visualization of their hands as play piano blindfolded or of the notes on the score. The additional bilateral activations in temporal areas likely hold the memorized representations of the melodic and harmonic structure of the concerto that subserve the auditory anticipations of the recalled composition, as well as recognition of the produced piano sounds. The responsive regions in posterior cingulate may mediate and monitor both the use of the memorized music composition and the unfolding contour of its implied emotive, interpretative, and expressive features. Strong thalamic activations may be instrumental in linking sensory and motor parameters for fine fingering and tone production. Activated regions in basal ganglia are likely subserving the selection and organization of segments of action, including timing. SMA, in which there is additional activation on the right beyond that for scales, is probably instrumental in coordinating the independence of the left hand. Dorsolateral premotor cortex is likely involved in the motor planning and programming for bimanual performance with increased control and coordination required for the Bach concerto. The additional activations in primary motor areas are involved in executing the more intricate and subtle plans for finger and sound production. The regions in posterior cerebellum may support aspects of auditory processing. The anterior cerebellum is likely supporting sensory processing associated with arm and finger movements. In addition, memorized musical performance is associated with deactivation of a range of areas whose engagement may detract from a fully realized performance. This network of areas and functions will need to be confirmed and refined by future studies.

Finally, a new view is also provided here of the brain areas specifically subserving the generation from memory of musical scales during performance. The representation of information used to generate the sequence of notes in a scale would appear to be very distinct from that for a musical composition, and should be reflected in the neural structures activated. The strongest foci were in posterior cingulate cortex, bilateral middle temporal cortex, right middle frontal gyrus (BA 9), and right precuneus (BA 7). Other activations were in right superior temporal cortex, left inferior frontal gyrus, right temporoparietal areas, right fusiform gyrus, right precuneus gyrus, and right prefrontal cortex (BA 10). Note that the Sergent et al. (1992) condition of playing (and hearing) scales, contrasted with listening to scales, produced increases in left primary motor cortex (BA 4: −35, −26, 54), left premotor cortex (BA 6: −4, −7, 57), and right (anterior) cerebellum (15, −62, −20). The two frontal activations were indistinguishable from ones observed here (−34, −22, 54; −6, −4, −50). Moreover, the cerebellar activation in the Sergent et al. study is reflected in bilateral activations here (culmen (V): −12, −52, −20; 22, −54, −22) and is likely related to the auditory and somatomotor production of two, rather one, scale melodies.

This distinctive network of activations suggests the following distributed functions. The cingulate may execute a controlling influence over initiation of the ordered string of notes in each scale. The bilateral middle temporal areas may hold auditory representations of scale information (a sequence of tone intervals and possibly a tonal center). The right middle frontal and left inferior frontal cortical areas may be involved in programming the sequential ordering of motor execution. The right precuneus, right temporoparietal, and fusiform areas may represent abstract visual–spatial association amongst notes, staves, and keys. These speculations should be assessed and refined in further experimentation.

The preceding comparisons of activated networks are delimited by the interplay of various differences in playing scales and the concerto. First, the performance of the Bach piece requires recalling more complicated information than does scales. Effects of this variable are probably apparent in the greater activation in auditory association areas (BA 22 and 21), posterior cingulate, and cuneus and lingual areas. Second, the concerto performance requires more intricate, controlled fingering and tone production. This factor is likely reflected in increases in thalamus, basal ganglia, SMA, insula, dorsolateral premotor cortex, and anterior cerebellum. Third, the concerto performance requires vividly conveying a comprehension of the musical structure (e.g., tonality, rhythm, dynamics, interpretative features, etc.). Effects of this factor may be observed in auditory areas (BA 38, 22, and 21), posterior cerebellum, posterior cingulate, cuneus, and lingual areas. Fourth, musical performance is associated with emotional responses, which are likely much more limited when playing scales. However, areas known to activate during emotional responses to music were not appreciably active here. Nonetheless, it is possible that activations related to emotional responses were in posterior cingulate, insula, and basal ganglia. Fifth, the concerto performance demands more attention than scales. This factor may be reflected in different ways here. There were no increases for the concerto in core attentional areas, but the effects may be more diffuse because there was more detected activation overall than for scales: nearly twice as many distinct foci and 72% greater overall extent of activation. Moreover, there was nearly 50% greater deactivation overall for the concerto performance than scales, an effect that may be related to a deepened focus of attention, as discussed earlier. It is conceivable then that both the greater activations and greater deactivations are related to differences in attention in the two performances. Finally, interactions amongst these variables in the present relatively naturalistic study need to be clarified by future studies aimed at comparing parametrically varied conditions operationalizing each factor. For example, planned studies contrast performances varying in musical complexity, while other factors are held relatively constant. These designs are analogous to studies of deduction (Parsons, Monti, Martinez, & Osherson, 2004) and syntactical processing (Stromswold, Caplan, Alpert, & Rauch, 1996).

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References

Aiello, R. (2001). Playing piano by heart: From behavior to cognition. In R. J. Zatorre & I. Peretz (Eds.), *The biological foundations of music* (pp. 389–393). New York: Annals of the New York Academy of Science.

Akshoomoff, N. A., Courchesne, E., & Townsend, J. (1997). Attention coordination and anticipatory control. In J. D. Schmahmann (Ed.), *The cerebellum and cognition* (pp. 575–598). New York: Academic Press.

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Science*, *4*, 267–278.

Bentovoglio, M., Kultas-Ilinsky, K., & Ilinsky, I. (1993). Limbic thalamus: Structure, intrinsic organization, and connections. In B. A. Vogt & M. Gabriel (Eds.), *Neurobiology of cingulate cortex and limbic thalamus* (pp. 71–122). Boston: Birkhauser.

Bihan, D. L., Turner, R., Zeffiro, T. A., Cuenod, C. A., Jezzard, P., & Bonnerat, V. (1993). Activation of human primary visual cortex during visual recall: A magnetic resonance imaging study. *Proceedings of the National Academy of Sciences*, *90*, 11802–11805.

Blood, A. J., & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Science*, *98*, 11818–11823.

Blood, A. J., Zatorre, R. J., Bermudes, P., & Evans, A. (1999). Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience*, *2*, 382–387.

Bower, J. M. (1997). Control of sensory data acquisition. In J. D. Schmahmann (Ed.), *The cerebellum and cognition* (pp. 490–513). New York: Academic Press.

Bower, J. M., & Parsons, L. M. (2003). Rethinking the lesser brain. *Scientific American*, *289*, 50–57.

Brown, S., Martinez, M. J., & Parsons, L. M. (2004). Passive music listening spontaneously engages limbic and paralimbic systems. *NeuroReport*, *15*, 2033–2037.

Brown, S., Parsons, L. M., Martinez, M. J., Hodges, D., & Fox, P. T. (in press). The song system of the human brain. *Cognitive Brain Research*, *20*, 363–375.

Cappelletti, M., Waley-Cohen, H., Butterworth, B., & Kopelman, M. (2000). A selective loss of the ability to read and write music. *Neurocase*, *6*, 332–341.

Carmichael, S. T., & Price, J. L. (1995). Limbic connections of the orbital and medial prefrontal cortex in macaque monkeys. *Journal of Comparative Neurology*, *363*, 615–641.

Carpenter, A. F., Georgopoulos, A. P., & Pellizzer, G. (1999). Motor control encoding of serial order in a context-recall task. *Science*, *283*, 1752–1757.

Chaffin, R., & Imreh, G. (2002). Practicing perfection: Piano performance as expert memory. *Psychological Science*, *13*, 342–349.

Chaffin, R., Imreh, G., & Crawford, M. (2002). *Practicing perfection: Memory and piano performance*. Mahway, NJ: Erlbaum.

Connors, B. W., Landisman, C. E., & Reid, R. C. (1998). Thalamus: Organization and function. *Trends in Neurosciences*, *21*, 539–540.

Crammond, D. J., & Kalaska, J. F. (1996). Differential relation of discharge in primary motor cortex and premotor cortex to movement versus actively maintained postures during a reaching task. *Experimental Brain Research*, *108*, 45–61.

Csikszentimihalyi, M., & Csikszentimihalyi, I. S. (1988). *Optimal experience: Psychological studies of flow in consciousness*. New York: Cambridge University Press.

D'Agostino, R. B., Belatner, A., & D'Agostino, R. B., Jr. (1990). A suggestion for using powerful and informative tests of normality. *American Statistician*, *44*, 316–321.

Duhamel, J.-R., Colby, C. L., & Goldberg, M. E. (1998). Ventral intraparietal area of the macaque: Congruent visual and somatic response properties. *Journal of Neurophysiology*, *79*, 126–136.

Egner, T., & Gruzelier, J. H. (2003). Ecological validity of neurofeedback: Modulation of slow wave EEG enhances musical performance. *NeuroReport*, *14*, 1221–1224.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, *270*, 305–307.

Evers, S., Dannert, J., Rodding, D., Rotter, G., & Ringelstein, E.-B. (1999). The cerebral hemodynamics of music perception: A trancranial Doppler sonography study. *Brain*, *122*, 75–85.

Faillenot, I., Toni, I., Decety, J., Gregoire, M. C., & Jeannerod, M. (1997). Visual pathways for object-oriented action and object recognition, functional anatomy with PET. *Cerebral Cortex*, *7*, 77–85.

Fiez, J. A., Petersen, S. E., Cheney, M. K., & Raichle, M. E. (1992). Impaired nonmotor learning and error-detection associated with cerebellar damage—A single case study. *Brain*, *115*, 155–178.

Fox, P. T., & Mintun, M. (1989). Noninvasive functional brain mapping by change-distribution analysis of averaged PET images of $H_2{}^{15}O$ tissue activity. *Journal of Nuclear Medicine*, *30*, 141–149.

Fox, P. T., Mintun, M., Reiman, E., & Raichle, M. E. (1988). Enhanced detection of focal brain responses using inter-subject averaging and change-distribution analysis of subtracted PET images. *Journal of Cerebral Blood Flow and Metabolism*, *8*, 642–653.

Friston, K. J., Frith, C. D., Liddle, P. R., & Frackowiak, R. S. J. (1991). Comparing functional (PET) images: The assessment of significant change. *Journal of Cerebral Blood Flow and Metabolism*, *11*, 690–699.

Gaab, N., Gaser, C., Zaehle, T., Jancke, L., & Schlaug, G. (2003). Functional neuroanatomy of pitch memory—An fMRI study with sparse temporal sampling. *NeuroImage*, *19*, 1417–1426.

Gaser, C., & Schlaug, G. (2003). Brain structures differ between musicians and non-musicians. *Journal of Neuroscience*, *23*, 9240–9245.

Grasby, P. M., Frith, C. D., Friston, K. J., Bench, C., Frackowiak, R. S. J., & Dolan, R. J. (1993). Functional mapping of brain areas implicated in auditory-verbal memory function. *Brain*, *1*(16), 1–20.

Graziano, M. S. A., Taylor, C. S. R., Moore, T., & Cooke, D. F. (2002). The cortical control of movement revisited. *Neuron*, *36*, 1–20.

Griffiths, T. D., Büchel, C., Frackowiak, R. S. J., & Patterson, R. D. (1998). Analysis of temporal structure in sound by the human brain. *Nature Neuroscience*, *1*, 422–427.

Griffiths, T. D., Johnsrude, I., Dean, J. L., & Green, G. G. R. (1999). A common neural substrate for the analysis of pitch and duration pattern in segmented sound? *NeuroReport*, *10*, 3825–3830.

Guillery, R. W. (2003). Branching thalamic afferents link action and perception. *Journal of Neurophysiology*, *90*, 539–548.

Hallett, M., & Grafman, J. (1997). Executive function and motor skill learning. In J. D. Schmahmann (Ed.), *The cerebellum and cognition* (pp. 297–323). New York: Academic Press.

Halpern, A. R., & Zatorre, R. J. (1999). When that tune runs through your head: A PET investigation of auditory imagery for familiar melodies. *Cerebral Cortex*, *9*, 697–704.

Haueisen, J., & Knosche, T. R. (2001). Involuntary motor activity in pianists evoked by music perception. *Journal of Cognitive Neuroscience*, *13*, 786–792.

Henson, R. N. A., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event related functional magnetic resonance imaging study. *Journal of Neuroscience*, *19*, 3962–3972.

Holcomb, H. H., Medoff, D. R., Caudill, P. J., Zhao, Z., Lahti, A. C., Dannahs, R. F., et al. (1998). Cerebral blood flow relationships associated with a difficult tone recognition task in trained normal volunteers. *Cerebral Cortex*, *8*, 534–542.

Houk, J. C., Davis, J. L., & Beiser, D. G. (Eds.). (1995). *Models of information processing in the basal ganglia*. Cambridge: MIT Press.

Hund-Georgiadis, M., & von Cramon, D. Y. (1999). Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals. *Experimental Brain Research*, *125*, 417–425.

Imamizu, H., Kuroda, T., Miyauchi, S., Yoshioka, T., & Kawato, M. (2003). Modular organization of internal models of tools in the human cerebellum. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 5461–5466.

Ivry, R. (1997). Cerebellar timing systems. In J. D. Schmahmann (Ed.), *The cerebellum and cognition* (pp. 556–573). New York: Academic Press.

Ivry, R. B., & Fiez, J. A. (2000). Cerebellar contributions to cognition and imagery. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed., pp. 999–1011). Cambridge, MA: MIT Press.

Janata, P. (2001). Brain electrical activity evoked by mental formation of auditory expectations and images. *Brain Topography*, *13*, 169–193.

Janata, P., Birk, J. L., Van Horn, J. D., Leman, M., Tillmann, B., & Bharucha, J. (2002). The cortical topography of tonal structures underlying western music. *Science*, *298*, 2167–2170.

Janata, P., & Grafton, S. T. (2003). Swinging in the brain: Shared neural substrates for behaviors related to sequencing and music. *Nature Neuroscience*, *6*, 682–687.

Jäncke, L., Shah, N. J., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cognitive Brain Research*, *10*, 177–183.

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*, 187–245.

Jeannerod, M. (1997). *The cognitive neuroscience of action*. Cambridge, MA: Blackwell.

Jeannerod, M. (2004). Visual and action cues contribute to the self-other distinction. *Nature Neuroscience*, *5*, 422–423.

Jog, M. S., Kubota, Y., Connolly, C. I., Hillegaart, V., & Graybiel, A. M. (1999). Building neural representations of habits. *Science*, *286*, 1745–1749.

Judd, T., Gardner, H., & Geschwind, N. (1983). Alexia without agraphia in a composer. *Brain*, *106*, 435–457.

Kermadi, I., & Joseph, J. P. (1995). Activity in caudate nucleus of monkey during spatial sequencing. *Journal of Neurophysiology*, *74*, 911–933.

Klein, I., Paradis, A. L., Poline, J. B., Kosslyn, S. M., & LeBihan, D. (2000). Transient activity in the human calcarine cortex during visual–mental imagery: An event-related fMRI study. *Journal of Cognitive Neuroscience*, *12*, 15–23.

Koelsch, S., Gunter, T. C., von Cramon, D. Y., Zysset, S., Lohman, G., & Friederici, A. D. (2002). Bach speaks: A cortical "language-network" serves the processing of music. *NeuroImage*, *17*, 956–966.

Krings, T., Tooper, R., Foltys, H., Erberich, S., Sparing, R., Willmes, K., et al. (2000). Cortical activation patterns during complex motor tasks in piano players and control subjects: A functional magnetic resonance imaging study. *Neuroscience Letters*, *278*, 189–193.

Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., et al. (2000). Automatic Talairach labels for functional brain mapping. *Human Brain Mapping*, *10*, 120–131.

Langheim, F. J., Callicott, J. H., Mattay, V. S., Duyn, J. H., & Weinberger, D. R. (2002). Cortical systems associated with covert music rehearsal. *NeuroImage*, *16*, 901–908.

Liu, Y., Pu, Y., Gao, J.-H., Parsons, L. M., Xiong, J., Liotti, M., et al. (2000). The human red nucleus and lateral cerebellum in cooperative roles supporting sensory discrimination. *Human Brain Mapping*, *10*, 147–159.

Mach, E. (1998). *Great contemporary pianists speak for themselves*. New York: Dover.

Maddock, R. J., Garrett, A. S., & Buonocore, M. H. (2001). Remembering familiar people: The posterior cingulate cortex and autobiographical memory retrieval. *Neuroscience*, *104*, 667–676.

Maddock, R. J., Garrett, A. S., & Buonocore, M. H. (2003). Posterior cingulate activation by emotional words: fMRI evidence from an emotional valence decision task. *Human Brain Mapping*, *18*, 30–41.

Marin, O. S. M., & Perry, D. W. (1992). Neurological aspects of musical processing. In D. Deutsch (Ed.), *Psychology of music* (2nd ed., pp. 653–724). New York: Academic Press.

Meister, I. G., Krings, T., Foltys, H., Boroojerdi, B., Muller, M., Topper, R., et al. (2004). Playing piano in the mind—An fMRI study on music imagery and performance in pianists. *Cognitive Brain Research*, *19*, 219–228.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Mintun, M., Fox, P. T., & Raichle, M. E. (1989). A highly accurate method of localizing regions of neuronal activity in the human brain with PET. *Journal of Cerebral Blood Flow and Metabolism*, *9*, 96–103.

Morris, R., Pandya, D. N., & Petrides, M. (1999). Fiber system linking the mid-dorsolateral frontal cortex with the retrosplenial/presubicular region in the rhesus monkey. *Journal of Comparative Neurology*, *407*, 183–192.

Munte, T. F., Altenmuller, E., & Jancke, L. (2002). The musician's brain as a model of neuroplasticity. *Nature Reviews: Neuroscience*, *3*, 473–478.

Nakada, T., Fujii, Y., Suzuki, K., & Kwee, I. L. (1998). 'Musical brain' revealed by high field (3 Tesla) functional MRI. *NeuroReport*, *9*, 3853–3856.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Pantev, C., Roberts, L. E., Schultz, M., Egnelien, A., & Ross, B. (2001). Timbre-specific enhancement of auditory cortical representations in musicians. *NeuroReport*, *12*, 169–174.

Parsons, L. M. (2003). Exploring the functional neuroanatomy of music performance, perception and comprehension. In R. J. Zatorre & I. Peretz (Eds.), *The cognitive neuroscience of music* (pp. 247–268). Oxford, UK: Oxford University Press.

Parsons, L. M., & Fox, P. T. (1997). Sensory and cognitive tasks. In J. D. Schmahmann (Ed.), *The cerebellum and cognition, international review of neurobiology: vol. 41* (pp. 255–272). San Diego: Academic Press.

Parsons, L. M., Hodges, D. A., & Fox, P. T. (1998). Neural basis of the comprehension of musical harmony, melody, and rhythm. Abstracts for Cognitive Neuroscience Society Annual Meeting. *Journal of Cognitive Neuroscience*.

Parsons, L. M., Monti, M., Martinez, M. J., & Osherson, D. A. (2004). Brain basis of deduction: Effects of argument validity and content. In *Society for Neuroscience Abstracts*.

Parsons, L. M., & Osherson, D. A. (2001). New evidence for distinct right and left brain systems for deductive and probabilistic reasoning. *Cerebral Cortex*, *11*, 954–965.

Parsons, L. M., & Thaut, M. H. (2001). Functional neuroanatomy of the perception of musical rhythm in musicians and non-musicians. Proceedings of the International Conference on Functional Mapping of the Human Brain. *NeuroImage*.

Passingham, R. E. (1993). *Frontal lobes and voluntary action*. New York: Oxford University Press.

Passingham, R. E. (1996). Functional specialization of the supplementary motor area in monkeys and humans. *Advances in Neurology*, *70*, 105–166.

Peretz, I., Blood, A. J., Penhune, V., & Zatorre, R. (2001). Cortical deafness to dissonance. *Brain*, *124*, 928–940.

Peretz, I., & Coltheart, M. (2003). Modularity of music processing. *Nature Neuroscience*, *7*, 688–691.

Perry, D. W., Zatorre, R. J., Petrides, M., Alivisatos, B., Meyer, E., & Evans, A. C. (1999). Localization of cerebral activity during simple singing. *NeuroReport*, *10*, 3979–3984.

Platel, H., Price, C., Baron, J. C., Wise, R., Lambert, J., Frackowiak, R. S., et al. (1997). The structural components of music perception. *Brain*, *120*, 243–299.

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 676–682.

Raichle, M. E., Martin, M. R. W., Herskovitch, P., Mintun, M. A., & Markham, J. (1983). Brain blood flow measured with intravenous $H_2{}^{15}O$. II. Implementation and validation. *Journal of Nuclear Medicine*, *24*, 790–798.

Redgrave, P., Prescott, T. J., & Gurney, K. (1999). The basal ganglia: A vertebrate solution to the selection problem? *Neuroscience*, *89*, 1009–1023.

Reiser, D. (Ed.). (1992). *Auditory imagery*. Mahwah, NJ: Erlbaum.

Riecker, A., Ackermann, H., Wildgruber, D., Dogil, G., & Grodd, W. (2000). Opposite hemispheric lateralization effects during speaking and singing at motor cortex, insula and cerebellum. *NeuroReport*, *11*, 1997–2000.

Sakata, H. (1996). Coding 3-D features of objects used in manipulation by parietal neurons. In R. Caminiti, K.-P. Hoffmann, F. Lacquaniti, & J. Altman (Eds.), *Vision and movement: Mechanisms in the cerebral cortex* (pp. 55–63). Strasbourg: Human Frontier Science Program.

Samson, S., & Zatorre, R. J. (1988). Melodic and harmonic discrimination following unilateral cerebral excision. *Brain and Cognition*, *7*, 348–360.

Satoh, M., Takeda, K., Nagata, K., Hatazawa, J., & Kuzuhara, S. (2001). Activated brain regions in musicians during an ensemble: A PET study. *Cognitive Brain Research*, *12*, 101–108.

Schmahmann, J. D., Doyon, J. A., McDonald, D., Holmes, C., Lavoie, K., Hurwitz, A., et al. (1999). Three-dimensional MRI atlas of the human cerebellum in proportional stereotaxic space. *NeuroImage*, *10*, 233–260.

Schneider, P., Scherg, M., Dosch, H. G., Specht, H. J., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschel's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature Neuroscience*, *5*, 688–694.

Schneider, R. J., Friedman, D. P., & Mishkin, M. (1993). A modality-specific somato-sensory area within the insula of the rhesus monkey. *Brain Research*, *621*, 116–120.

Schon, D., Anton, J. L., Roth, M., & Besson, M. (2002). An fMRI study of music reading. *NeuroReport*, *13*, 2285–2289.

Schurmann, M., Raij, T., Fujiki, N., & Hari, R. (2002). Mind's ear in a musician: Where and when in the brain. *NeuroImage*, *16*, 434–440.

Sergent, J. (1993). Mapping the musician brain. *Human Brain Mapping*, *1*, 20–38.

Sergent, J., Zuck, S., Terriah, & McDonald, B. (1992). Distributed neural network underlying musical sight-reading and keyboard performance. *Science*, *257*, 106–109.

Stewart, L., Henson, R., Kampe, K., Walsh, V., Turner, R., & Frith, U. (2003). Brain changes after learning to read and play music. *NeuroImage*, *20*, 71–83.

Stewart, L., & Walsh, V. (2001). Music of the hemispheres. *Current Biology*, *11*, R125–R127.

Stromswold, K., Caplan, D., Alpert, N., & Rauch, S. (1996). Localization of syntactic comprehension by positron emission tomography. *Brain and Language*, *52*, 452–473.

Strother, S. C., Lang, N., Anderson, J. R., Schaper, K. A., Rehm, K., Hansen, L. K., et al. (1997). Activation pattern reproducibility: Measuring the effects of group size and data analysis models. *Human Brain Mapping*, *5*, 312–316.

Suzuki, W. A., & Amaral, D. G. (1994). Perirhinal and parahippocampal cortices of the macaque monkey: Cortical afferents. *Journal of Comparative Neurology*, *350*, 497–533.

Talairach, J., & Tournoux, P. (1988). Co-planar stereotaxic atlas of the human brain. 3-Dimensional proportional system: an approach to cerebral imaging. New York: Thieme.

Tanji, J., & Shima, K. (1994). Role for supplementary motor area cells in planning several movements ahead. *Nature*, *371*, 413–416.

Ullen, F., Forssberg, H., & Ehrsson, H. H. (2003). Neural networks for the coordination of the hands in time. *Journal of Neurophysiology*, *89*, 1126–1135.

Vogt, B. A., Finch, D. M., & Olson, C. R. (1992). Functional heterogeneity in cingulate cortex: The anterior executive and posterior evaluative regions. *Cerebral Cortex*, *2*, 435–443.

Vogt, B. A., & Gabriel, M. (Eds.). (1993). *Neurobiology of cingulate cortex and limbic thalamus*. Boston: Birkhauser.

Vokaer, M., Bier, J. C., Elincx, S., Claes, T., Paquier, P., Goldman, S., et al. (2002). The cerebellum may be directly involved in cognitive functions. *Neurology*, *58*, 967–970.

Warrier, C. M., & Zatorre, R. J. (2004). Right temporal cortex is critical for utilization of melodic contextual cues in a pitch constancy task. *Brain*, *127*, 1616–1625.

Zatorre, R. J. (1985). Discrimination and recognition of tonal melodies after unilateral cerebral excisions. *Neuropsychologia*, *23*, 31–41.

Zatorre, R. J. (2003). Neural specialization for tonal processing. In I. Peretz & R. Zatorre (Eds.), *The cognitive neuroscience of music* (pp. 231–246). Oxford: Oxford University Press.

Zatorre, R. J., & Belin, P. (2001). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex*, *11*, 946–953.

Zatorre, R. J., Evans, A. C., & Meyer, E. (1994). Neural mechanisms underlying melodic perception and memory for pitch. *Journal of Neuroscience*, *14*, 1908–1919.

Zilles, K., Schlaug, G., Matelli, M., Luppino, G., Schleider, A., Qu, M., et al. (1995). Mapping of the human and macaque sensorimotor areas by integrating architectonic, transmitter receptor, MRI, and PET data. *Journal of Anatomy*, *187*, 515–537.