Cerebral Cortex August 2006;16:1157-1167
doi:10.1093/cercor/bhj057
Advance Access publication October 12, 2005

The Neural Basis of Human Dance

Steven Brown[1,2], Michael J. Martinez[1] and Lawrence M. Parsons[1,3]

[1]Research Imaging Center, University of Texas Health Science Center at San Antonio, San Antonio, TX, USA
[2]Present address: Department of Psychology, Simon Fraser University, Burnaby, BC, Canada
[3]Present address: Department of Psychology, University of Sheffield, Sheffield, UK

Human dance was investigated with positron emission tomography to identify its systems-level organization. Three core aspects of dance were examined: entrainment, meter and patterned movement. Amateur dancers performed small-scale, cyclically repeated tango steps on an inclined surface to the beat of tango music, without visual guidance. Entrainment of dance steps to music, compared to self-pacing of movement, was supported by anterior cerebellar vermis. Movement to a regular, metric rhythm, compared to movement to an irregular rhythm, implicated the right putamen in the voluntary control of metric motion. Spatial navigation of leg movement during dance, when controlling for muscle contraction, activated the medial superior parietal lobule, reflecting proprioceptive and somatosensory contributions to spatial cognition in dance. Finally, additional cortical, subcortical and cerebellar regions were active at the systems level. Consistent with recent work on simpler, rhythmic, motor-sensory behaviors, these data reveal the interacting network of brain areas active during spatially patterned, bipedal, rhythmic movements that are integrated in dance.

Keywords: complex sensorimotor coordination, dance, entrainment, music, neuroimaging

Introduction

Many natural, complex sensorimotor activities involve the integration of rhythm, spatial pattern, synchronization to external stimuli and coordination of the whole body. Such activities include old evolutionary adaptations such as hunting, fighting and play, as well as more recent ones such as group physical labor, marching, musical performance and sport. Neuroimaging studies have examined some components of these complex actions, such as the entrainment of movement to external timekeepers or spatial patterning of limb movement. However, this research has typically studied elementary processes such as ankle rotation or finger tapping (e.g. Penhune *et al*., 1998; Lutz *et al*., 2000; Debaere *et al*., 2001; Ehrsson *et al*., 2003; Sahyoun *et al*., 2004). A central issue is whether the neural systems implicated in these elementary processes ‘scale up’ and ‘scale out’ to complex ecological activities. Are the mechanisms controlling complex sensorimotor processes the same ones as those that underlie elementary processes like ankle rotation and finger tapping or are new mechanisms recruited? For example, dance is a complex sensorimotor action: do known elementary processes underlying simple movements ‘scale up’ to rhythmically timed, spatially patterned whole-body movements seen in human dance? The aim of the present study was to explore these and related issues in the context of examining for the first time the neural basis of dance.

Dance is a universal human behavior, one associated with group rituals (Sachs, 1937; Farnell, 1999). Although it is depicted in cave art from more than 20 000 years ago (Appenzeller, 1998), dance may be much more ancient than that. Dance may in fact be as old as the human capacities for bipedal walking and running, which date back 2–5 million years (Ward, 2002; Bramble and Lieberman, 2004). One of the principal properties of dance is that body movements are organized into spatial patterns. This patterning of movement encompasses a trajectory map of the body in exocentric space (Longstaff, 2000) as well as a kinesthetic and visual map of the body schema in egocentric space (Haggard and Wolpert, 2005). The displacement patterns of dance can involve any body part; every dance can be characterized by the identity and number of its participating movement-units. In addition, dances tend to be modular in organization, being composed of discrete sections that are concatenated or interleaved with one another cyclically. Because of this combinatoric organization, dances are amenable to grammatical analysis and description (Hutchinson-Guest, 1997).

A second property of dance is the synchronization of movements with timekeepers such as musical beats, a capacity that is apparently specific to humans. Indeed, it is striking how our bodies can spontaneously move in response to a musical beat. Virtually all dancing is done to musical rhythms, thereby permitting a temporal synchronization among dancers. Dance gestures generally mirror the hierarchical arrangement of strong and weak beats found in musical rhythm patterns. In waltz music, for example, the first beat is stressed while the second and third beats are weaker; likewise in waltz movements, the first step is the broadest and most forceful, while the second and third steps are shorter and weaker. Thus, the entrainment of dance to music not only involves synchronization in time but a spatial element related to equating hierarchies in the motor pattern with those in the musical rhythm.

We conducted a positron emission tomography (PET) study with amateur dancers performing small-scale, bipedal dance steps on an inclined surface, as compared to auditory, motor and rhythmic control tasks. In addition to working towards a systems-level view of the neural basis of the complex sensorimotor processes underlying dance, we attempted to isolate the foregoing individual processes, using planned comparisons in a subtractive design. First, we sought to localize brain areas involved in the synchronization of leg movement to the rhythm of an auditory stimulus. For this, we made a planned comparison of patterned leg movement performed to a musical beat (Metric condition) with a matched motor pattern performed in a self-paced though metric manner without an external timekeeper (Motor condition). A second goal was to identify the brain areas involved in the voluntary control of metric movements, that is, dance steps occurring in an equal-time-interval rhythm. For this, we made a planned comparison of patterned leg movement paced to music possessing a regular, metric rhythm (Metric condition) with that paced to music possessing a highly irregular, unpredictable rhythm (Non-Metric condition). Finally, we sought to isolate the neural basis of spatial patterning of lower-limb movement by making a planned comparison of the conditions in which the legs moved in space (Metric condition) with a condition in which the leg muscles contracted isometrically but without leg movement, also to a metric rhythm (Contractions condition). By controlling for parameters related to muscle contraction, we expected this contrast to reveal brain areas supporting spatial cognition in dance, especially as related to the lower extremities. Two control conditions involved passive listening to music (Listening condition) and eyes-closed rest.

Materials and Methods

Subjects

Five male and five female amateur dancers, with a mean age of 33.8 years (range 19–46 years), participated in the study after giving their informed consent (in accord with the Declaration of Helsinki and the Institutional Review Board of the University of Texas Health Science Center). Each individual was without neurological or psychiatric illness. All participants were right-handed, as confirmed by the Edinburgh Handedness Inventory. Nine of the 10 subjects indicated that they would use their right leg to kick a ball (Elias and Bryden, 1998). The subjects were currently active amateur tango dancers, with a mean of 8.5 years of recent recreational dance experience, of which 2.5 years were of Argentine tango (range 1–4 years) and the remainder was of a wide variety of other dance forms (e.g. Latin, ballroom, ballet). In spite of these individual differences in age and years of overall dance experiences, the dancers were of comparable proficiency in Argentine tango and in the relatively simple tango tasks used in the study. The subjects had minimal musical experience.

Stimuli

Commercial recordings of instrumental Argentine tango songs, with a typical tempo of 60 beats per minute, were presented for the tasks containing music. All songs were matched for instrumentation, tempo and tonality, and were presented to subjects using CoolEdit (Syntrillium) from a laptop computer. For the Non-Metric condition, songs were edited to produce an irregular and unpredictable beat but without altering the average tempo (i.e. each song had an equal number of accelerations and decelerations of the tempo at random junctures). The stimuli for the listening condition were Greek 'rembetika' songs that were matched for the tempo, instrumentation and tonality of the tango songs. By using music other than tango songs, we sought to minimize the tendency for stimuli to elicit motor imagery of the dance steps performed in the movement tasks (see Ehrsson *et al.*, 2003). The activations observed for this condition, as contrasted to rest, are described elsewhere (Brown *et al.*, 2004).

Tasks

The tasks involved the performance of simple bipedal dance movements on a laminated grid (see Procedure). The subjects were trained to be proficient at these dance steps in advance of the scanning session, so very little motor learning likely occurred during the experiment. Six conditions were tested, all of them with the eyes closed: (i) a patterned leg movement synchronized to the beat of metric, regularly timed tango music (Metric); (ii) the same patterned leg movement executed to the beat of non-metric, irregularly timed tango music (Non-Metric); (iii) a matched, patterned leg movement performed with no music (Motor); 4) a condition of isometric leg-muscle contractions synchronized to the beat of metric tango music but with no leg displacement, in which the left and right leg-muscles contract in alternation (Contractions); 5) passive music listening with no movement (Listening); and (vi) silent motionless 'Rest'. Subjects experienced little visual stimulation during trials, as they were lying in a dimly light room with their eyes closed. The dance step for the metric and non-metric conditions consisted of a simple 6-step box pattern (Fig. 1*a*, left panel) — derived from the basic 'salida' step of the Argentine tango — that involved alternation of the left and right feet. The pattern for the Motor condition (Fig. 1*a*, right panel) was different from that of the Metric and Non-Metric conditions in order to minimize the use of mental imagery of the music from the latter two tasks. For the Metric, Non-Metric and Contractions conditions, subjects were instructed to take one step or make one leg-muscle contraction per strong beat of the music, be that to a metric or non-metric rhythm. For the Motor condition, there was no music for the movement to be entrained to, but subjects were instructed to practice the step, and were given feedback to either quicken or slow the movement if their tempo was too dissimilar from that of the Metric condition. As per instruction, and as verified by observation and feedback, all foot movement occurred in a smooth gliding manner on the surface rather than in a stepping manner; the feet never completely lifted off the surface.

Procedure

While lying supine in the PET scanner, subjects flexed their knees ~90° and placed their feet on a stable, flat, smooth surface, which was inclined ~30° above the horizontal (Fig. 1*b*). The surface was laminated to reduce friction during foot movement and to minimize compensatory body or head movement. Subjects wore stockings to further reduce friction. Each big toe was visibly marked to facilitate coding of foot position on a grid with centimeter markings, as recorded using a camcorder. The music stimuli were presented via headphones to the subject.

Behavioral Analysis

Behavioral analysis of the rate and extent of videotaped leg movement was performed by one of the authors (M.J.M.) for the three movement tasks from the 40 s PET scan. First, the dance steps were performed quite accurately, often with 1 cm of error. Second, the mean number of steps during the 40 s task interval in the Metric, Non-Metric and Motor conditions was 34.5 ± 4.0, 40.9 ± 8.5 and 36.0 ± 1.3 (mean ± SD). There was no difference in the rates between the Metric and Motor conditions ($P > 0.05$). However, the average movement rate for Non-Metric dance was higher than that for the other two conditions, indicating that the dancers misinterpreted some secondary beats as primary ones; subjects were most likely susceptible to such errors because tango music is highly syncopated. Third, the perimeter of the triangular movement-path outlined by each foot during the dance tasks was measured. The means across the two feet for the Metric, Non-Metric and Motor conditions were 38.1 ± 8.1, 39.5 ± 6.9 and 30.5 ± 6.4 cm^2. The perimeter values for the self-paced dance task were significantly shorter than those for the other two tasks. In absolute terms, this amounted to a difference of ~0.7 cm in each direction, which is small compared to the overall extent of movement (on the order of 6 cm in each direction). The shorter paths likely relate to the use of a different pattern for the Motor condition compared to the other two. This matched pattern was designed so as to preserve the same combination of foot movements (forward, backward, left and right) as the pattern for Metric and Non-Metric. Movement extent for these patterns was not predictable *a priori*. There was no relationship between years of tango experience and age of subject with respect to performance in the scanner as measured by rate of stepping and by extent and accuracy of steps during the task (data not shown). A correlation analysis of the relationship between movement perimeter and regional cerebral blood flow failed to find significant covariance with any of the observed activations.

Imaging

During the PET session, the subject's head was immobilized using a closely fitted thermal-plastic facial mask with openings for the eyes, ears, nose and mouth. Auditory stimuli were presented through ear-pieces taped over the subjects' ears. During scanning, subjects were instructed to close their eyes and to minimize head and body movement as much as possible. During a session in advance of the scan date and during a practice session on the day of the scan, subjects practiced performing the dance steps in a highly controlled manner while minimizing head movement. Subjects had two PET scans for each of the six tasks. Each scanning session began with the Motor task, and the

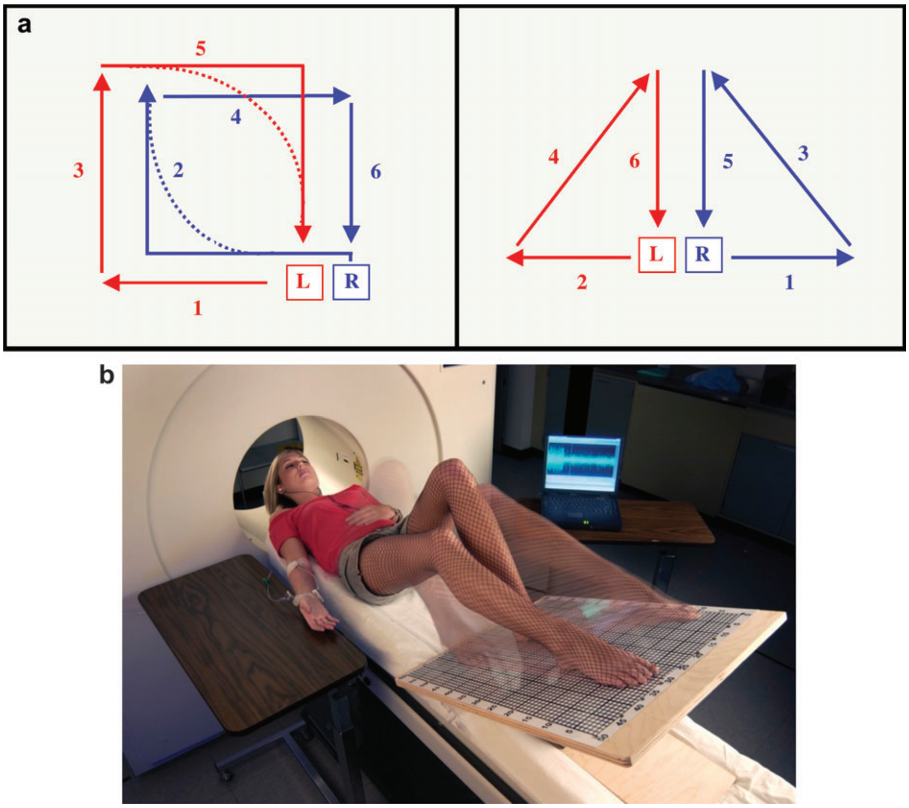

Figure 1. (*a*) The dance steps consisted of six-step movements in which the left and right legs always alternated (see Materials and Methods). The pattern in the left panel was used for the Metric and Non-Metric dance tasks; the other pattern was used for the self-paced dance task (Motor). The dotted lines in the left panel show the path of each limb as it passes near a position stepped to by the other limb. (*b*) A subject illustrating the dance task.

tasks were thereafter counterbalanced across subjects such that one replication of each task was performed before the next set began. Subjects began each task 30 s prior to injection of the $H_2^{15}O$ bolus. Bolus uptake required ~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 auditory stimulus was terminated and the subject was asked to discontinue the task and lie still during an immediately following 50 s scan.

Image Analysis

Positron emission tomography was performed with a CTI HR+ camera, which had a pixel spacing of 2.0 mm, an inter-plane, center-to-center distance of 2.4 mm and 63 transaxial scan planes. Images were reconstructed using a Hanning filter with a cut off frequency of 0.5, resulting in images with a spatial resolution of ~4.3 mm (full-width at half-maximum). The data were smoothed with an isotropic 10 mm Gaussian kernel. Anatomical MRI data was acquired with an Elscint 1.9 T Prestige system with an in-plane resolution of 1 mm^2 and 1.5 mm slice thickness. Convex-hull spatial normalization was performed prior to group subtraction ($n = 10$) using 'change distribution analysis' methods (Raichle *et al.*, 1983; Fox *et al.*, 1988; Mintun *et al.*, 1989). Thus, significant changes in cerebral blood flow indicating neural activity were detected with a region-of-interest-free image subtraction strategy. Intra-subject image averaging was performed within conditions (Fox *et al.*, 1988). Images were spatially normalized (Fox *et al.*, 1985) into proportional, bicommissural coordinate space relative to the Talairach atlas (Talairach and Tournoux, 1988) using spatial normalization performed by using SN. Inter-scan, intra-subject movement was assessed and corrected using the Woods' algorithm (Woods *et al.*, 1993). A search algorithm (Mintun *et al.*, 1989) was used to identify local extrema within a 5 × 5 × 5 voxel search cube. A beta-2 statistic measuring kurtosis and a beta-1 statistic measuring skewness of the extrema histogram (Fox *et al.*, 1988) were used as omnibus tests to assess overall significance (D'Agostino *et al.*, 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 *et al.*, 1988, 2001). The areas of significant change were mapped into 3D stereotactic space. Pixel-based statistical analyses (Xiong *et al.*, 1996) were used to assess the statistical significance of outliers identified in the subtracted images, pixel-by-pixel. Cluster Analysis was performed to identify regional changes (Xiong *et al.*, 1996). Gross anatomical labels were applied to the detected local maxima using a volume-occupancy-based, anatomical-labeling strategy as implemented in the Talairach Daemon (Lancaster *et al.*, 2000), with activations in cerebellum labeled with reference to the Schmahmann *et al.* (2000) atlas. In the change distribution analysis method, the pooled variance of all brain voxels is used as the reference for computing significance, and is distinct from methods that compute the variance at each voxel. This method is more sensitive (Strother *et al.*, 1997), particularly for small samples, than voxel-wise variance methods (e.g. Friston *et al.*, 1991). The critical-value threshold for regional effects is not raised to correct for multiple comparisons because omnibus statistics are established before post-hoc analysis. Statistical maps were overlaid onto group mean anatomical MRI and thresholded at $Z > 4.27$, $P < 0.00001$ (one tailed).

The analyses of functional images for factors in our experimental design were conducted employing the following planned comparisons. A systems-level view of dancing to music was analyzed by comparing Metric and Rest conditions. The functional neuroanatomy of movement entrainment was analyzed by comparing Metric and Motor conditions, Metric and Music conditions, and Music and Rest conditions. Metric movement was analyzed by comparing Metric and Non-Metric conditions. Spatial pattern of leg movement was analyzed by contrasting Metric and Non-Metric, respectively, with the Contractions conditions. Spatial patterning of movement was also examined in the comparison of Motor and rest conditions. Finally, to eliminate spurious activations resulting from the subtractions of deactivations, we verified every activation in each higher-level contrast by examination of the relevant condition from rest.

Results

A systems-level view of the brain areas contributing to comparatively natural, although supine, dance performance (Metric dancing minus Rest, Table 1) revealed activations in bilateral motor, somatosensory and premotor areas, right supplementary motor area, right frontal operculum, left medial superior parietal cortex, superior temporal regions, right cingulate motor area, basal ganglia, and bilateral anterior vermal and posterior-lateral cerebellum. The following planned and *post hoc* comparisons examine the specific subsystems activated during dance. There were no significant differences detected between male and female dancers in the profiles of activations across conditions (data not shown).

Entrainment of Movement to Music

When dance in a self-paced manner without music (Motor) was subtracted from dance entrained to a musical beat (Metric), the principal signal for this subtraction outside of auditory areas was seen in the vermis of anterior cerebellar lobule III (Fig. 2, Table 2). This activation was also present in the analysis of each task minus rest. These data implicate the anterior vermis in entrainment of movement to music. No such increases for entrainment were observed in other regions activated in common between entrained and self-paced dancing, such as sensorimotor, premotor, superior parietal, cingulate or frontal opercular areas. The increase in vermal activity for entrained dancing was not due to the addition of the accompanying music *per se*, as the subtraction of music listening from metric dance had no effect on the intensity of the anterior vermal activity (not shown). In addition, this latter subtraction, while eliminating all activity in cortical auditory areas found in both the music-listening condition alone and in entrained dance minus self-paced dance, revealed a significant signal in the right medial geniculate nucleus (Fig. 3*a*,*b*). The medial geniculate nucleus was not active during self-paced dance without music. Moreover, metric dance minus self-paced dance and, especially, metric dance minus music listening revealed activity in lateral and vermal aspects of posterior left cerebellar lobules V and VI (Figs 2 and 3*b*). As suggested later, audiomotor entrainment may be mediated through the transmission of coarsely processed beat information from subcortical auditory areas to the cerebellum.

Metric Movement

In comparing the dance condition entrained to a metric rhythm with a dance condition entrained to an irregular rhythm (Table 3), we observed a strong signal bilaterally in the putamen for the metric condition, with an emphasis in the right putamen (see Fig. 4, which shows this same pattern when each condition is contrasted with rest). This activity appeared to occur in the somatotopic representation of the leg (Maillard *et al.*, 2000). No such basal ganglia activation was detected for non-metric dance. By contrast, in non-metric dance minus rest, a strong activation was seen in right ventral thalamus, specifically, in the ventral posterior nucleus bordering on the pulvinar. This area was not

Table 1
Stereotaxic coordinates and z-score values for activations in the Metric dance condition contrasted to Rest

Hemisphere	Region	*x*	*y*	*z*	*Z*-score
Frontal					
Right	Premotor/primary motor cortex (4/6)	6	−26	60	9.68
	Premotor cortex (6)	0	−12	56	6.70
	SMA rostral (6)	6	−6	62	5.78
	Frontal operculum (44)	54	8	6	4.54
Left	Premotor/primary motor cortex (4/6)	−4	−20	66	8.76
Parietal					
Left	Superior parietal lobule (5/7)	−4	−46	62	6.88
Temporal					
Right	Superior temporal gyrus (42)	60	−20	8	4.65
	Superior temporal gyrus (22)	37	−26	6	4.54
	Temporal pole/planum polare (38)	45	12	−4	4.62
Left	Superior temporal gyrus (42)	−48	−20	8	4.54
Other					
Right	Cingulate sulcus (24/31)	8	−6	44	5.46
	Putamen	28	−4	6	5.00
Cerebellum					
Right	Lobule IV	16	−36	−20	5.82
	Lobule IX	14	−54	−52	5.68
	Lobule V	28	−36	−28	5.61
	Lobule IV	16	−44	−15	5.54
Left	Anterior vermis lobule III	0	−48	−16	9.78
	Lobule VIIIB	−18	−50	−52	6.49
	Lobule IV	−22	−38	−26	6.10
	Lobule V/VI	−24	−50	−25	4.93
	Lobule VI	−14	−76	−20	4.58

For all tables, Talairach atlas coordinates are in millimeters along the left–right (*x*), anterior–posterior (*y*) and superior–inferior (*z*) axes. In parentheses after each brain region is the approximate Brodmann area, except in the case of the cerebellum, in which the anatomical labels of Schmahmann *et al.* (2000) are used. The intensity threshold for this table is $Z > 4.27$, $P < 0.00001$ (one-tailed).

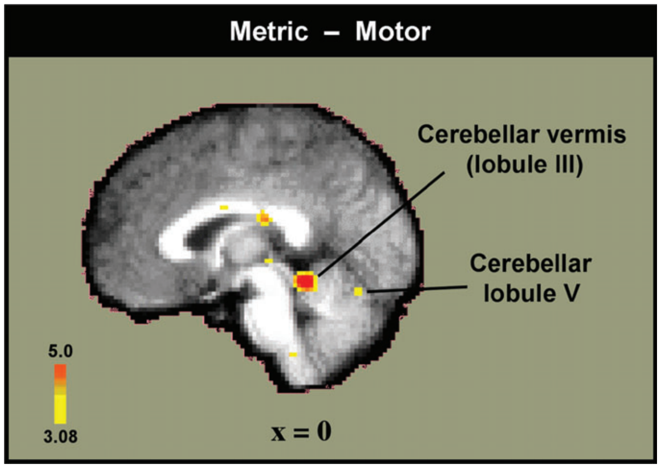

Figure 2. The activation (−2, −44, −12) in anterior cerebellar vermis (lobule III) in the analysis of Metric dance minus Motor. Also shown is the activation in lobule V. The group mean activations are shown registered onto an averaged brain in all figures. The right side of the figure is the right side of the brain in all figures. At the left end of the figure is a color scale for the intensity of the activations. The intensity threshold in Figures 2–5 is $Z > 2.58$, $P < 0.005$ (one-tailed).

Table 2
Stereotaxic coordinates and *Z*-score values for activations in the Metric dance condition contrasted to Motor, and contrasted to Music

Hemisphere	Region	*x*	*y*	*z*	*Z*-score
Metric–Motor					
Right	Superior temporal gyrus (22)	58	−24	6	6.68
	Superior temporal gyrus (22)	54	−6	2	5.05
	Superior temporal gyrus (22)	46	−20	6	4.98
Left	Primary auditory cortex (22)	−38	−26	4	5.05
	Superior temporal pole (38)	−42	2	−12	4.87
	Anterior vermis lobule III	−2	−44	−12	6.02
Metric–Music					
Right	Anterior vermis lobule III	2	−48	−16	10.12

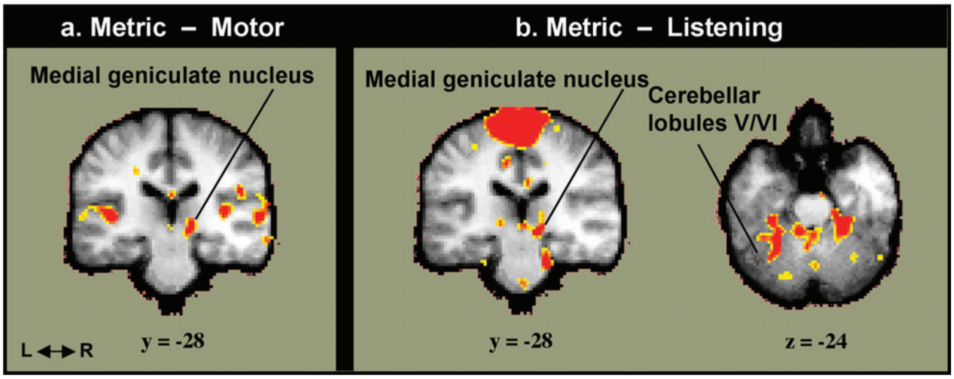

Figure 3. (*a*) Activation in the medial geniculate nucleus in the analyses of Metric dance minus Motor and (*b*) Metric dance minus music Listening. The peak coordinate for the medial geniculate nucleus in the former subtraction is at (14, –28, –4) whereas that for the latter is at (14, –30, –6). Activity in cerebellar lobule V and VI in the analysis of Metric dance minus music Listening. In coronal and axial views throughout, the left side of the image represents the left side of the brain.

Table 3

Stereotaxic coordinates and *Z*-score values for activations in the Metric dance condition contrasted to Non-Metric, and vice versa

Hemisphere	Region	*x*	*y*	*z*	*Z*-score
Metric–Non-Metric					
Right	Posterior cingulate (31)	4	−64	28	4.81
	Anterior cingulate (32)	6	32	−8	4.66
	Putamen	27	−3	8	4.63
Non-Metric–Metric					
Right	Superior temporal gyrus (22)	52	−30	6	5.53
	Thalamus	17	−22	8	4.71
	Anterior cerebellum lobule IV	10	−48	−20	4.82

activated above threshold for metric dance. To explore this pattern of findings, we noted that in a *post hoc* comparison there were intermediate levels of activity in both putamen and thalamus observed in the performance of both self-paced dancing without music (Motor) and isometric leg-muscle contractions to music (Contractions condition) (Fig. 4, legend). This overall pattern points to a reciprocal relationship in activity between the putamen and ventral thalamus, with metric movement exhibiting strong putamen and weak thalamus responses, and non-metric movement showing the reverse profile. This reciprocity may be causal, as mediated, for example, by the indirect pathway of the basal ganglia circuit, where the ventral thalamus is the major output structure of the basal ganglia (e.g. Rao *et al.*, 1997). Alternatively, it may be incidental, mediated through the intervention of other structures. In either case, the results suggest that the putamen is preferentially activated by movement patterns that are regular and predictable, and that irregular and unpredictable patterns activate other pathways, including those containing the ventral thalamus.

Spatial Patterning of Leg Movement

The analysis of metric dance minus the contractions condition (where the leg muscles were contracted isometrically in an alternating fashion to the beat of metric tango music but without there being leg movement along the surface) revealed activity in the medial portion of the superior parietal lobule [Brodmann's area (BA) 5/7; precuneus] (Fig. 5, Table 4). Superior parietal activity was equally strong in the subtraction of the contractions condition from either metric dancing or non-metric dancing and for self-paced dancing minus rest, thereby suggesting that this area is specifically involved in spatial guidance of leg movement independent of temporal parameters related to movement timing or entrainment. The dance tasks were performed quite accurately without visual guidance (see Behavioral Analysis), and thus the foregoing activations suggest that the medial superior parietal lobule encodes proprioceptive or somatosensory information about spatial coordinates for leg movement.

Activations seen in each of the movement tasks (minus rest) occurred in the primary motor and sensory cortices (paracentral lobule), premotor cortex, supplementary motor area (SMA), and somatotopic leg areas of the cerebellum (lobules IV and VIII) (Fig. 5; see Table 1 for the coordinates of these activations in metric dance minus rest). In addition, the right frontal operculum (BA 44/6) — near the right-hemisphere homologue of Broca's area — was activated in all of the tasks involving motor production (minus rest) but not in passive music listening (Fig. 6). Because the intensity of this activation did not vary in each of the movement tasks (minus rest), we attribute its function more to motor sequencing in general (Ehrsson *et al.*, 2000; Janata and Grafton, 2003) than to spatial patterning of limb movement. Finally, activation in the cingulate motor area was also detected for all of the motor conditions (minus rest), although much more so for the movement conditions than for the condition of isometric leg-muscle contractions (see the middle panel of Fig. 5). This activity likely reflects a somatotopic map in this region, as the dorsal bank of the cingulate sulcus in monkeys contains a leg representation, and electrical stimulation of this region leads to hindlimb movement (Luppino *et al.*, 1991).

Discussion

These findings illustrate the coordination of distributed neural systems that underlie bipedal, cyclically repeated dance steps entrained to a musical rhythm. The functional subsystems can be summarized as follows. The superior temporal gyrus and superior temporal pole represent the melodic and harmonic aspects of the heard music. In parallel, the medial geniculate nucleus appears to send inputs, via brainstem relay nuclei, to the anterior cerebellar vermis and lobules V and VI regarding beat information, to support the entrainment of movement to a musical beat. The basal ganglia, and particularly the putamen, subserve the selection and organization of segments of action,

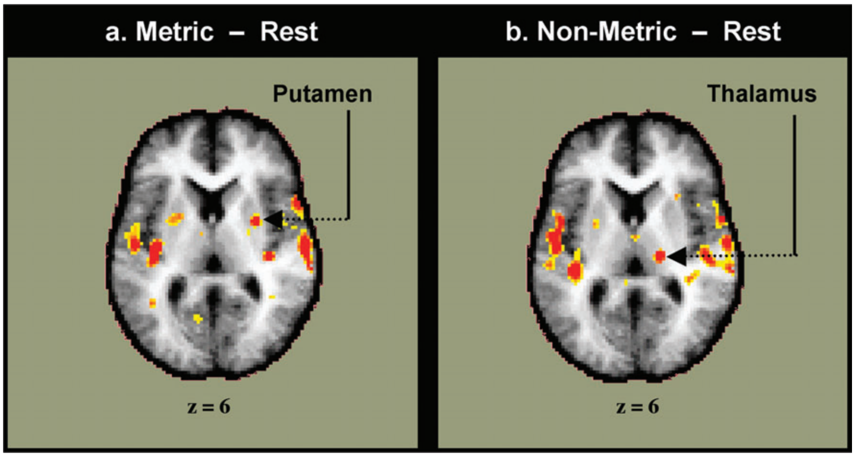

Figure 4. Reciprocal activation in the putamen and ventral thalamus in Metric and Non-Metric dance. The thalamic activation occurs at the junction of the ventral posterior and pulvinar nuclei. Direct subtraction of Non-Metric from Metric retains the activation in the putamen, and direct subtraction of Metric from Non-Metric retains the activation in the thalamus (not shown). The *Z*-score values for the putamen and ventral thalamus, respectively, for the four motor conditions were: Metric (5.00, 2.49), Non-Metric (undetectable, 5.78), Motor (3.44, 3.10) and Contractions (3.27, 3.19).

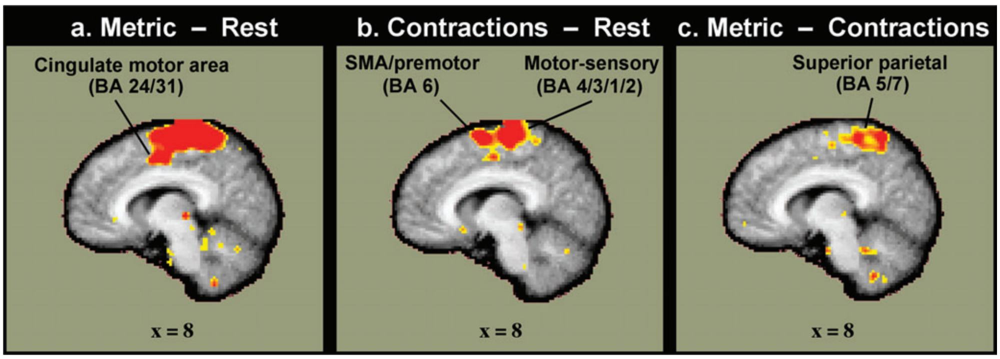

Figure 5. Metric dance minus leg-muscle Contractions eliminates the activations in the premotor and motor-sensory cortices, and leaves signal in the superior parietal lobule, spanning the medial part of BA 5 and 7 (precuneus). Activation in the cingulate motor area is seen to be just above threshold. The activations in the motor-sensory cortex and SMA/premotor cortex are bilateral even though the figure shows only one hemisphere. The mesial motor strip comprised of SMA/premotor cortex and motor-sensory cortex is active in (*a*) and (*b*). (*c*) The peak coordinate of the anterior focus in the precuneus is (8, –56, 60).

especially for movements having strong predictability and regularity, such as metrically timed movements. The thalamus is involved in linking somatosensory and motor parameters, and is particularly important for novel or non-metric rhythms. Somatotopic areas for the lower extremity in motor, premotor and SMA regions encode parameters related to muscle group, contractile force, initial and final position, and movement direction. The SMA, cingulate motor area and possibly the cerebellum support interhemispheric coordination of the two limbs during cyclically repeated, bipedal motion. The right frontal operculum is involved in motor sequencing, while the right cingulate motor area processes aspects of movement intention and the allocation of motor resources. Finally, medial aspects of the superior parietal lobule subserve kinesthetically mediated spatial guidance of leg movement during navigation in dance. This network of brain areas controlling dance will require confirmation and refinement in future studies.

There was a trend for right-hemisphere dominance for many of our unilateral activations, including the frontal operculum, cingulate motor area, putamen, ventral thalamus and medial geniculate nucleus, along with a corresponding focus in the left cerebellar vermis. Although no such trend has been observed

Table 4

Stereotaxic coordinates and *Z*-score values for activations in the Metric dance condition contrasted to Contractions

Hemisphere	Region	*x*	*y*	*z*	*Z*-score
Metric–Contractions					
Right	Superior parietal lobule (5/7)	8	−56	60	4.96
	Posterior cerebellum lobule VIIIB	22	−50	−48	4.82
Left	Superior Parietal lobule (5/7)	−2	−48	60	5.52
	Superior parietal lobule (5/7)	−6	−58	54	4.61
	Anterior vermis lobule III	−2	−50	−18	6.46
	Posterior cerebellum lobule IX	−14	−44	−56	6.18
Non-Metric–Contractions					
Right	Superior parietal lobule (5/7)	4	−48	60	5.23
	Pulvinar	18	−24	10	4.73
	Putamen	32	−16	−6	4.48
	Anterior cerebellum lobule IV	10	−44	−26	5.28
	Anterior cerebellum lobule IV	8	−48	−20	5.01
	Anterior cerebellum lobule III	−16	−34	−17	4.83
Left	Precuneus (7)	−18	−54	46	5.53
	Paracentral lobule (5)	−8	−40	54	5.35
	Medial frontal gyrus (6)	−20	−12	50	5.35
	Superior parietal lobule (7)	−12	−52	56	5.05
	Posterior cerebellum lobule VIIIB	−12	−46	−54	5.21
	Anterior cerebellum lobule V	−28	−40	−32	5.11
	Anterior cerebellum lobule III	−16	−40	−24	4.55
	Anterior cerebellum lobule IV	−16	−46	−24	4.38

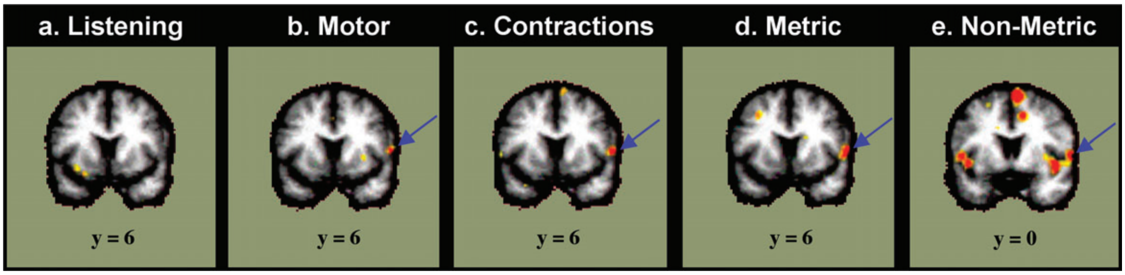

Figure 6. Cerebral blood flow increases in the right frontal operculum (BA 44, see arrows) during the four motor tasks but not music listening. The peak voxel for Motor minus Rest is at (54, 6, 8), for Contractions minus Rest is at (54, 6, 6), and for Metric minus Rest is at (54, 8, 6). The activation in the Non-Metric minus Rest subtraction was slightly more posterior to those for the preceding three conditions and mapped more onto BA 6 than BA 44, with a peak voxel at (58, 0, 6).

for natural gait (Fukuyama *et al.*, 1997; Miyai *et al.*, 2001), a study that compared flexion/extension of the ankle, flexion/extension of the wrist and finger movement, all on the right side of the body (Luft *et al.*, 2002), found that knee movement was accompanied by strong ipsilateral activation in the primary motor cortex and primary sensory cortex. Likewise, a study of imagined or executed flexion/extension of the toes (Ehrsson *et al.*, 2003) reported right frontal operculum activation for right-sided movements.

In addition, recent studies of postural deficits in stroke patients suggest the presence of a distributed system, primarily in the right hemisphere, for representing trunk posture relative to the environment (e.g. Spinazzola *et al.*, 2003). Further research will be needed to clarify the extent to which horizontal placement of the body during the dance tasks might have contributed to our observed right-hemisphere lateralization effects. In future, studies may be able to circumvent the neuroimaging constraints that currently prevent an investigation of important issues such as upright whole-body movements and interpersonal coordination processes involved in pair dancing (e.g. as in celebrated instances of Rogers doing Astaire's steps backward and in high heels).

In the following comments, we discuss these observations in more detail, with a view toward assessing how the mechanisms observed in paradigms focusing on controlled elementary processes 'scale up' to those for the more complex natural activity of dancing. At a general level, we note that elements of both discrete and rhythmic movements (Schaal *et al.*, 2004) are present in dance, itself a gestural system. As such, the patterns of activations we observed are broadly consistent with the possibility that the subcortical systems activated are involved in the timing and coordination of discontinous movements, whereas the specific cortical systems activated here may be supporting the control of the continuous movements (Miall and Ivry, 2004).

Sensorimotor Entrainment

Three key facets of dance were selectively analyzed in our study design: audiomotor entrainment, meter and patterning of movement. For the first facet, a comparison between two matched dance patterns performed at the same rate — one requiring entrainment to a musical beat and the other one self-paced — highlighted the importance of the anterior cerebellar vermis (central lobule, III), but not other parts of the motor or sensory system, to entrainment processing. The vermal activation was equally strong in the Metric and Non-Metric dance conditions (data not shown), both of which were based on temporal entrainment. This suggests that the vermis functions in entrainment per se, independent of the nature of the temporal pattern being entrained to. Very similar activations have been observed in recent studies of repetitive lower-limb movement entrained to metric cues in either auditory or visual form. In a functional magnetic resonance imaging (fMRI) study of right-foot flexion/extension timed to a metric auditory cue (Debaere *et al.*, 2001), activity was detected in the anterior cerebellar vermis (3, –45, –18, as compared to 0, –48, –16 here), as it was in a similar fMRI study of right-foot flexion/extension timed to a metric visual cue (Sahyoun *et al.*, 2004; i.e. 2, –48, –20, as compared to 0, –48, –16 here). This region was also activated by rhythmic self-paced walking (Fukuyama *et al.*, 1997: 0, –50, –20, as compared to 0, –48, –16 here) and finger tapping without an ongoing external stimulus (Penhune *et al.*, 1998: 8, –48, –21 and 1, –50, –15, as compared to 0, –48, –16 here). These similarities between the controlled elementary paradigms and dancing imply that common mechanisms are involved in entrainment.

This pattern of data highlights the importance of the anterior cerebellar vermis (III) for the entrainment of movement to external timing cues. Interestingly, in our analysis of functional activation data for metric dance minus passive music listening, activity in cortical auditory areas was eliminated, leaving behind a significant signal in the right medial geniculate nucleus as well as posterior cerebellar lobules V and VI. These regions were not found to be activated during self-paced dance steps performed without music (when contrasted to rest). There are substantial reciprocal projections between the thalamic nuclei and cerebellum via brainstem relays (see reviews in Schmahmann, 1997). In addition, cerebellar lobules V and VI have been specifically implicated in neuroimaging studies of pitch and melody discrimination, as dissociated from motor coordination or cortical motor activity (e.g. Holcomb *et al.*, 1998; Griffiths *et al.*, 1999; Gaab *et al.*, 2003; Parsons, 2003a; Petacchi *et al.*, 2005). It is thus possible that the sensory input to the anterior cerebellar vermis for entrainment processing involves coarsely processed auditory information from subcortical sites. If so, this would imply that entrainment in dance does not require higher-level musical content (e.g. tonality, harmony, timbre) but may simply depend on low-level beat information, as mediated by subcortical pathways. This hypothesis may in part account for the sharing of entrainment mechanisms between dance and simple sensorimotor behaviors like finger tapping and ankle rotation.

There is strenuous ongoing debate about the function of the cerebellum, which was classically viewed as a motor-control and coordination structure only but which has recently been implicated in non-motor processes by a wide range of findings (e.g. see reviews in Schmahmann, 1997; Ivry and Fiez, 2000; Rapoport *et al.*, 2000; Vokaer *et al.*, 2002; Bower and Parsons, 2003). The following three hypotheses of cerebellar function are likely to be most pertinent to the findings of this study. One account assumes that the cerebellum embodies internal forward-inverse model pairs (Wolpert *et al.*, 1998); in the present case, such model pairs would need to include the sensory aspects of movement, the movements *per se* and perception of the auditory beat. Another account (Ivry, 1997) emphasizes the role of cerebellum in supporting timing processes in both the preparation and coordination of motor responses (in vermal and anterior cerebellum) and the sensory perception of duration on the order of hundreds of milliseconds (in lateral cerebellum). In a third view, the role of the cerebellum is to optimize the control of the acquisition of sensory data (Bower, 1997; Bower and Parsons, 2003). In the current case, the cerebellum would be hypothesized to assist cortical, subcortical and peripheral neural structures in collecting optimal auditory and somatosensory information in order to influence the cortical motor system to better synchronize the execution of movement with the auditory rhythm. Further research is needed to clarify the functions of the foregoing cerebellar regions.

Metric and Non-metric Movement

Another principal feature of our results was seen in the contrast between dance steps entrained to a metric rhythm and the same steps entrained to a non-metric rhythm. We found that metric dance movement induced strong activity bilaterally in the putamen, and especially the right putamen. Non-metric dance movement, in contrast, showed no activity in the putamen but instead displayed a strong signal in the right ventral thalamus. A variety of prior research affirms a role for the basal ganglia in the control of metric movement in rhythmic tapping tasks (e.g. Rao *et al.*, 1997; Penhune *et al.*, 1998) and in piano performance of memorized musical pieces (Parsons *et al.*, 2005). The involvement of the putamen in metric movement is supported by an fMRI study of visually cued, metric right-foot flexion/extension (Sahyoun *et al.*, 2004); the thalamus was much less active. Likewise, in a PET study of the same task (Ehrsson *et al.*, 2000), activity in the putamen, but not the thalamus, was reported. The involvement of the ventral thalamus in non-metric rhythms agrees with similar findings from an fMRI study (Lutz *et al.*, 2000) of tapping the right index finger to a non-metric, randomly timed visual cue (−20, −16, 12, as compared to 18, −24, 8 here).

Overall, the reciprocal activity between putamen and ventral thalamus just described suggests that for both dance and elementary movements, the basal ganglia are preferentially activated in the execution of motor activities having a regular, predictable rhythm and that unpredictable unfamiliar temporal patterns recruit other pathways. This is also congruent with an fMRI study of self-paced finger tapping showing that the basal ganglia were principally active for simple rhythms and that their activity decreased with greater rhythmic complexity, whereas the thalamus (and anterior cerebellar vermis) increased in activation with increasing complexity (Dhamala *et al.*, 2003). In our study, intermediate levels of activity in both the putamen and ventral thalamus were seen for both self-paced dancing without music and for the performance of isometric leg-muscle contractions to metric tango music. Thus, activity in the basal ganglia circuit is modulated by limb displacement and entrainment as well as by the presence or absence of metric regularity. This complex functionality suggests that the basal ganglia might be one part of the brain sensitive to the interactions amongst entrainment, meter and spatial patterning specifically seen in dance.

Somatotopy and Control of Lower Limbs

The third principal aspect of our data highlights the topographic representation of the lower extremity in the motor-sensory cortex as well as in the superior parietal lobule, cingulate motor area, cerebellum, and putamen. Activation of a mesial strip encompassing the leg representation in the primary motor cortex, somatosensory cortex, SMA and premotor cortex was present for all four tasks involving motor activity. Activations in very similar somatotopic regions for the lower extremity have been found in a number of reports using a variety of techniques and paradigms, including the following: a SPECT study of upright walking (Fukuyama *et al.*, 1997); a near-infrared spectroscopy study of bipedal walking on a treadmill (Miyai *et al.*, 2001); an fMRI study of right-foot flexion/extension timed to a metric auditory cue (Debaere *et al.*, 2001); a PET study of this same task (Ehrsson *et al.*, 2000); an fMRI study of metric, visually cued right-foot flexion/extension (Sahyoun *et al.*, 2004); an fMRI study of unipedal flexion/extension of either the left or right knee joint (Luft *et al.*, 2002); an fMRI study of the placement of either foot into visually presented foot postures (Chaminade *et al.*, 2005); and an fMRI study of imagined and executed flexion/extension of the toes timed to a metric auditory cue (Ehrsson *et al.*, 2003). The foregoing motor, premotor, and SMA areas most likely encode parameters related to muscle group, contractile force, initial and final position, and movement direction (Graziano *et al.*, 2002). The SMA, the cingulate motor area and possibly the cerebellum (Ivry, 1997; Wolpert *et al.*, 1998) are likely involved in interhemispheric coupling supporting cyclically repeated coordination of the two homologous limbs, as suggested by studies of bimanual coordination (e.g. Jäncke *et al.*, 2000). Very similar activations were observed for coordinated unilateral movements of the hand and foot (Ehrsson *et al.*, 2000; Debaere *et al.*, 2001).

The right frontal operculum (BA 44/6) was activated by the four tasks involving motor production but not by music listening, suggesting a general role for this area in motor sequencing rather than a specific role in either spatial patterning or metric entrainment. Responses in the frontal operculum were observed in an fMRI study (Ehrsson *et al.*, 2003) of flexion/extension of the toe timed to a metric auditory cue (56, 8, 4 and 56, 8, 0, as compared to 54, 8, 6 here), both during mental imagery of movement and actual movement. Comparable activity was also reported in an fMRI study of visually cued metric right-foot flexion/extension (Sahyoun *et al.*, 2004). In a PET study of finger tapping timed to imitate the rhythm of brief sequences of visual stimuli with long or short elements (Penhune *et al.*, 1998), the right frontal operculum was also activated (46, 18, 3, as compared to 54, 8, 6 here). In addition, this region shows activations for motor mental imagery, perception, and imitation tasks involving the hands (Parsons *et al.*, 1995; Grafton *et al.*, 1996; Heiser *et al.*, 2003). Equally pertinent, a region anterior to this one was activated in ballet dancers while observing ballet movements and in capoeira dancers while observing capoeira movements (peaking at Talairach coordinates 54, 35, 1: Calvo-Merino *et al.*, 2005), thereby demonstrating expertise-dependent activity in the frontal operculum. These results support a role for this region in both elementary motor sequencing and in dance, during both perception and production. This activation pattern may also bear on new functional hypotheses that propose supralinguistic sequencing and syntax operations for the region broadly defined as Broca's region and its right homologue.

The right cingulate motor area (cingulate sulcus) was activated in all four motor tasks, with trends toward larger extents in the three tasks requiring movement of the legs. Similar activity was observed in an fMRI study (Sahyoun *et al.*, 2004) of visually cued metric right-foot flexion/extension (6, 14, 44 and −10, −6, 48, as compared to 8, −6, 44 here). The location of this activation corresponds to cytoachitectonic area 24dd (Vogt and Vogt, 2003), which in monkeys contains a topographic representation of the hindlimb and lower trunk (Luppino *et al.*, 1991; Rizzolatti *et al.*, 1996). This area may encode aspects of movement intention and the allocation of motor resources (Ball *et al.*, 1999), processes required in both elementary motor activities and in dance.

Spatial Cognition

Our findings suggest that the medial superior parietal lobule (BA 5/7, precuneus) plays a role in kinesthetic guidance of leg movement during navigation in dance, interacting with the foregoing motor, somatosensory, timing and sequencing areas. Activation in the medial superior parietal lobule was also observed in an fMRI study of right-foot flexion/extension (Debaere *et al.*, 2001) timed to a metric auditory cue (−3, −42, 69, as compared to −4, −46, 62 here), as well as in a similar PET study (Ehrsson *et al.*, 2000: −10, −45, 68, as compared to −4, −46, 62) that included a condition in which the right foot and right hand were simultaneously flexed or extended (−8, −47, 66, as compared to −4, −46, 62). In addition, the area was activated in a PET study of the tactile discrimination (without visual guidance) of parallel-piped objects pressed against the planta (Young *et al.*, 2004).

Posterior parietal cortex is regarded as subserving a variety of spatial cognitive functions (Colby and Goldberg, 1999; Parsons, 2003b) including those related to body schema (Berlucchi and Aglioti, 1997; Halligan *et al.*, 2003). The inferior and superior parietal lobules receive both somatosensory and visual inputs. The posterior parts of both lobules process visual information, the anterior superior parietal lobule processes somatosensory information, and the anterior inferior parietal lobule integrates somatosensory and visual information (Rizzolatti *et al.*, 1997; Colby and Olsen, 2003). The performance of dance steps with the eyes closed was reported by some of our subjects to be accompanied by mental imagery of their body. Thus, the foregoing parietal activation was likely involved in spatial cognitive functions based on proprioceptive processing of leg position and joint angle and on somatosensory contact of the feet with the surface (Parsons, 1987). Little is known about leg representations in posterior parietal cortex of either humans or monkeys. The monkey homologue of BA 5, area PE, contains leg representations (Rizzolatti *et al.*, 1996). PE is a high-level somatosensory area that does not receive visual inputs and that projects to primary motor cortex. Studies of hand movement find that PE neurons encode limb location in space using a body-centered coordinate system (Lacquaniti *et al.*, 1995). Thus, the medial superior parietal lobule may possess a map of peripersonal (egocentric) space based on proprioceptive cues related to lower limb position. Somesthetic guidance of navigation is key to dance, where vision provides a support role indicating whether space is sufficient to carry out particular movements. The fact that superior parietal lobule is activated in some of the studies of elementary ankle and wrist rotation discussed earlier might suggest that, unlike isometric muscle contraction, these simple movements still have a basic element of spatial patterning to them, simple though it might be. This suggests that activity in this region increases as the spatial and navigational demands of the movement increase.

Conclusion

Dance, like numerous natural, complex sensorimotor activities (e.g. sport, group physical labor, and musical performance), requires the integration of spatial pattern, rhythm, synchronization to external stimuli and whole-body coordination. Our findings suggest that many of the brain areas activated for dance are also recruited in elementary sensorimotor activities. However, the present methods can only show proximity or overlap in the location of neural activity. These results set the stage for more precise techniques that compare the detailed neural computations (e.g. Gold and Shadlen, 2001) performed in regions localized in common for simpler and more complex sensorimotor activities. Moreover, the present findings are based on observations of relatively skilled dancers who are well practiced at performing the dance steps in the study. Thus, our data do not reveal the role of learning in organizing the various elementary and complexity-related neural mechanisms. It is likely that learning or refinement of natural complex tasks would entail changes in functional and effective connectivity, and in the reorganization and redistribution of processes (Garraux *et al.*, 2005; Kelly and Garavan, 2005). Indeed, we observed greater variety and number of anterior cerebellar activations during the most unfamiliar condition (Non-Metric, Table 4), suggesting a role in adjusting fine, complex sensorimotor coordination to relatively novel entrainment signals (Ivry, 1997; Wolpert *et al.*, 1998; Bower and Parsons, 2003). Future studies will surely harvest significant information from studies of these and other aspects of complex natural activities.

Our findings specifically elucidate for the first time the neural systems and subsystems that underlie dance. These observations imply that dance, as a universal human activity, involves a complex combination of processes related to the patterning of bipedal motion and to metric entrainment to musical rhythms. More broadly, this study brings us closer to a richer understanding of the neural and psychological bases of complex, species-specific creative and artistic behaviors. This study is part of a contemporary wave of research exploring new neuroscientific hypotheses in the context of activities such as musical performance, drawing, visual aesthetics, dance observation and the viewing of cinematic narratives (Ino *et al.*, 2003; Kawabata and Zeki, 2003; Makuuchi *et al.*, 2003; Cela-Conde *et al.*, 2004; Hassan *et al.*, 2004; Calvo-Merino *et al.*, 2005; Parsons *et al.*, 2005).

Notes

We thank Julie Grezes, Petr Janata, Katz Sakai and two anonymous reviewers for very helpful comments on this manuscript. This research was supported by grants from the ChevronTexaco Foundation and the International Foundation for Music Research.

Address correspondence to Lawrence Parsons, Department of Psychology, University of Sheffield, Western Bank, Sheffield S10 2TP, UK. Email: L.parsons@sheffield.ac.uk.

References

Appenzeller T (1998) Evolution or revolution. Science 282:1451–1454.

Ball T, Schreiber A, Feige B, Wagner M, Lucking CH, Kristeva-Fega R (1999) The role of higher-order motor areas in voluntary movement as revealed by high resolution EEG and fMRI. Neuroimage 10:682–694.

Berlucchi G, Aglioti S (1997) The body in the brain: neural bases of corporeal awareness. Trends Neurosci 20:560–564.

Bower JM (1997) Control of sensory data acquisition. In: The cerebellum and cognition (Schmahmann JD, ed.), pp. 490–513. New York: Academic Press.

Bower JM, Parsons LM (2003) Rethinking the lesser brain. Sci Am 289:50–57.

Bramble, DM, Lieberman, DE (2004) Endurance running and the evolution of *Homo*. Nature 432:345–352.

Brown S, Martinez MJ, Parsons LM (2004) Passive music listening spontaneously engages limbic and paralimbic systems. Neuroreport 15:2033–2037.

Calvo-Merino B, Glaser DE, Grezes J, Passingham PE, Haggard P (2005) Action observation and acquired motor skills: an fMRI study with expert dancers. Cereb Cortex 15:1243–1249.

Cela-Conde CJ, le Marty G, Maestu F, Ortiz T, Munar E, Fernandez A, Roca M, Rossello J, Quesney F (2004) Activation of the prefrontal cortex in the human visual aesthetic perception. Proc Nat Acad Sci USA 101:6321–6325.

Chaminade T, Meltzoff AN, Decety J (2005) An fMRI study of imitation: action representation and body schema. Neuropsychologia 43:115–127.

Colby CL, Goldberg ME (1999) Space and attention in parietal cortex. Annu Rev Neurosci 22:319–349.

Colby CL, Olson CR (2003) Spatial cognition. In: Fundamental neuroscience, 2nd edn (Squire LR, Bloom FE, McConnell SK, Roberts JL, Spitzer NC, Zigmond MJ, eds), pp. 1229–1247. San Diego, CA: Academic.

Debaere F, Swinnen SP, Beatse E, Sunaert, S, Van Hecke P, Duysens J (2001) Brain areas involved in interlimb coordination: a distributed network. Neuroimage 14:947–958.

D'Agostino RB, Belatner A, and D'Agostino RB Jr. (1990). A suggestion for using powerful and informative tests of normality. Am Statistician 44:316–321.

Dhamala M, Pagnoni G, Wiesenfeld K, Zink CF, Martin M, Berns GS (2003) Neural correlates of the complexity of rhythmic finger tapping. Neuroimage 20:918–926.

Ehrsson HH, Naito E, Geyer S, Amunts K, Zilles K, Forssberg H, Roland PE (2000) Simultaneous movements of upper and lower limbs are coordinated by motor representations that are shared by both limbs: a PET study. Eur J Neurosci 12:3385–3398.

Ehrsson HH, Geyer S, Naito E (2003) Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. J Neurophysiol 90:3304–3316.

Elias LJ, Bryden MP (1998) Footedness is a better predictor of language lateralization than handedness. Laterality 3:41–51.

Farnell B (1999) Moving bodies, acting selves. Annu Rev Anthropol 28:341–373.

Fox PT, Perlmutter JS, Raichle ME (1985) Stereotactic localization for positron emission tomography. J Cereb Blood Flow Metab 9:141–153.

Fox PT, Mintun M, Reiman E, and Raichle ME (1988) Enhanced detection of focal brain responses using inter-subject averaging and change-distribution analysis of subtracted PET images. J Cereb Blood Flow Metab 8:642–653.

Fox PT, Huang A, Parsons LM, Xiong JH, Zamarripa F, Lancaster JL (2001) Location-probability profiles for the mouth region of human primary motor-sensory cortex: model and validation. Neuroimage 13:196–209.

Friston KJ, Frith CD, Liddle PR, Frackowiak RSJ (1991) Comparing functional (PET) images: the assessment of significant change. J Cereb Blood Flow Metab 11:690–699.

Fukuyama H, Ouchi Y, Matsuzaki S, Nagahama Y, Yamauchi H, Ogawa M, Kimura J, Shibasaki H (1997) Brain functional activity during gait in normal subjects: a SPECT study. Neurosci Lett 228:183–186.

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.

Garraux G, McKinney C, Wu T, Kansuku K, Nolte G, Hallett M (2005) Shared brain areas but not functional connections controlling movement timing and order. J Neurosci 25:5290–5297.

Gold JI, Shadlen MN (2001) Neural computations that underlie decisions about sensory stimuli. Trends Cogn Sci 5:10–16.

Grafton ST, Arbib MA, Fadiga L, Rizzolatti G (1996) Localization of grasp representation in human by PET. 2. Observation versus imagination. Exp Brain Res 112:103–111.

Graziano MS, Taylor CS, Moore T, Cooke DF (2002) The cortical control of movement revisited. Neuron 36:349–362.

Griffiths TD, Johnsrude I, Dean JL, Green GGR (1999) A common neural substrate for the analysis of pitch and duration pattern in segmented sound? NeuroReport 10:3825–3830.

Haggard P, Wolpert DM (2005) Disorders of body scheme. In: Higher-order motor disorders (Freund H-J, Jeannerod M, Hallett M, Leiguarda RC, eds), pp. 261–272. Oxford: Oxford University Press.

Halligan PW, Fink GR, Marshall JC, Vallar G (2003) Spatial cognition: evidence from visual neglect. Trends Cogn Sci 7:125–133.

Hassan U, Nir Y, Levy I, Fuhrmann G, Malach R (2004) Intersubject synchronization of cortical activity during natural vision. Science 303:1634–1640.

Heiser M, Iacoboni M, Maeda F, Marcus J, Mazziotta JC (2003) The essential role of Broca's area in imitation. Eur J Neurosci 17:1123–1128.

Holcomb HH, Medoff DR, Caudill PJ, Zhao Z, Lahti AC, Dannahs RF, Tamminga CA (1998) Cerebral blood flow relationships associated with a difficult tone recognition task in trained normal volunteers. Cereb Cortex 8:534–542.

Hutchinson-Guest A (1973) Labanotation: The system of analyzing and recording movement. Philadelphia, PA: Taylor and Frances, Inc.

Ino T, Asada T, Ito J, Kimura T, Fukuyama H (2003) Parieto-frontal networks for clock drawing revealed with fMRI. Neurosci Res 45:71–77.

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

Ivry RB, Fiez JA (2000) Cerebellar contributions to cognition and imagery. In: The new cognitive neurosciences, 2nd edn (Gazzaniga MS, ed.), pp. 999–1011. Cambridge, MA: MIT Press.

Janata P, Grafton ST (2003) Swinging in the brain: shared neural substrates for behaviors related to sequencing and music. Nat Neurosci 6:682–687.

Jäncke L, Peters M, Himmelbach M, Nösselt T, Shah J, Steinmetz H (2000) fMRI study of bimanual coordination. Neuropsychologia 38:164–174.

Kawabata H, Zeki S (2003) Neural correlates of beauty. J Neurophysiol 91:1699–1705.

Kelly, AMC, Garavan, H (2005) Human functional neuroimaging of brain changes associated with practice. Cereb Cortex 15:1089–1102.

Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R (1995) Representing spatial information for limb movement: role of area 5 in the monkey. Cereb Cortex 5:391–409.

Lancaster JL, Woldorff MG, Parsons LM, Liotti M, Freitas CS, Rainey L, Kochunov PV, Nickerson D, Mikiten SA, Fox PT (2000) Automatic Talairach labels for functional brain mapping. Hum Brain Mapp 10:120–131.

Longstaff JS (2000) Re-evaluating Rudolf Laban's choreutics. Percept Motor Skills 91:191–210.

Luft AR, Smith GV, Forrester L, Whitall J, Macko RF, Hauser T-K, Goldberg AP, Hanley, DF (2002) Comparing brain activation associated with isolated upper and lower limb movement across corresponding joints. Hum Brain Mapp 17:131–140.

Luppino G, Matelli M, Camarda R, Gallese V, Rizzolatti G (1991) Multiple representations of body movements in mesial area 6 and the adjacent cingulate cortex: an intracortical microstimulation study. J Comp Neurol 311:463–482.

Lutz K, Specht K, Shah NJ, Jancke L (2000) Tapping movements according to regular and irregular visual timing signals investigated with fMRI. Neuroreport 11:1301–1306.

Maillard L, Ishii K, Bushara K, Waldvogel D, Schulman AE, Hallett M (2000) Mapping the basal ganglia: fMRI evidence for somatotopic representation of the face, hand, and foot. Neurology 55:377–383.

Makuuchi M, Kaminaga T, Sugishita M (2003) Both parietal lobes are involved in drawing: a functional MRI study and implications for constructional apraxia. Cogn Brain Res 16:338–347.

Miall RC, Ivry R (2004) Moving to a different beat. Nature Neurosci 7:1025–1026.

Mintun M, Fox PT, Raichle ME (1989) A highly accurate method of localizing regions of neuronal activity in the human brain with PET. J Cereb Blood Flow Metab 9:96–103.

Miyai I, Tanabe HC, Sase I, Eda H, Oda I, Konishi I, Tsunazawa Y, Suzuki T, Yanagida T, Kubota K (2001) Cortical mapping of gait in humans: a near-infrared spectroscopic topography study. Neuroimage 14:1186–1192.

Parsons LM (1987) Imagined spatial transformation of one's hands and feet. Cogn Psychol 19:178–241.

Parsons, LM (2003a) Exploring the functional neuroanatomy of music performance, perception, and comprehension. In: The cognitive neuroscience of music (Peretz I, Zatorre RJ, eds), pp. 247–268. Oxford: Oxford University Press.

Parsons LM (2003b) Superior parietal cortices and varieties of mental rotation. Trend Cogn Sci 17:515–517.

Parsons LM, Fox PT, Downs JH, Glass T, Hirsch T, Martin C, Jerabek P, Lancaster JL (1995) Use of implicit motor imagery for visual shape discrimination as revealed by PET. Nature 375:54–59.

Parsons LM, Sergent J, Hodges DA, Fox PT (2005) Brain basis of piano performance. Neuropsychologia 43:199–215.

Penhune VB, Zatorre RJ, Evans AC (1998) Cerebellar contributions to motor timing: a PET study of auditory and visual rhythm reproduction. J Cogn Neurosci 10:752–765.

Petacchi A, Laird AR, Fox PT, Bower JM (2005) Cerebellum and auditory function: an ALE meta-analysis of functional neuroimaging studies. Hum Brain Mapp 25:118–128.

Raichle ME, Martin MRW, Hersovitch P, Mintun MA, and Markham J (1983) Brain blood flow measured with intravenous $H_2^{15}O$. II. Implementation and validation. J Nucl Med 24:790–798.

Rao SM, Harrington DL, Haaland KY, Bobholz JA, Cox RW, Binder JR (1997) Distributed neural systems underlying the timing of movements. J Neurosci 17:5528–5535.

Rapoport M, van Reekum R, Mayberg H (2000) The role of the cerebellum in cognition and behavior: a selective review. J Neuropsychiatry Clin Neurosci 12:193–198.

Rizzolatti G, Luppino G, Matelli M (1996) The classic supplementary motor area is formed by two independent areas. Adv Neurol 70:45–56.

Rizzolatti G, Fogassi L, Gallese V (1997) Parietal cortex: from insight to action. Curr Opin Neurobiol 7:562–567.

Sachs C (1937) World history of the dance. New York: Norton.

Sahyoun C, Floyer-Lea A, Johansen-Berg H, Mathews PM (2004) Towards an understanding of gait control: brain activation during the anticipation, preparation, and execution of foot movements. Neuroimage 21:568–575.

Schaal S, Sternad D, Osu R, Kawato M (2004) Rhythmic arm movement is not discrete. Nat Neurosci 7:1137–1144.

Schmahmann JD (ed.) (1997) The cerebellum and cognition. New York: Academic Press.

Schmahmann JD, Doyon JA, Toga AW, Petrides M, Evans AC (2000) MRI atlas of the human cerebellum. San Diego, CA: Academic Press.

Spinazzola, L, Cubelli, R, Della Sala, S (2003) Impairments of trunk movements following left or right hemispheric lesions: dissociation between apraxic errors and postural stability. Brain 126:2656–2666.

Strother SC, Lang N, Anderson JR, Schaper KA, Rehm K, Hansen LK, Rottenberg DA (1997) Activation pattern reproducibility: measuring the effects of group size and data analysis models. Hum Brain Mapp 5:312–316.

Talairach J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. New York: Thieme.

Vokaer M, Bier JC, Elincx S, Claes T, Paquier P, Goldman S, Bartholome EJ, Pandolfo M (2002) The cerebellum may be directly involved in cognitive functions. Neurology 58:967–970.

Vogt BA, Vogt, L (2003) Cytology of human dorsal midcingulate and supplementary motor cortices. J Chem Neuroanat 26:301–309.

Ward, CV (2002) Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? Yb Phys Anthro 35:195–215.

Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. Trends Cogn Sci 2:338–347.

Woods R, Mazziotta J, Cherry S (1993) MRI-PET registration with automated algorithm. J Comput Assist Tomogr 17:536–546.

Xiong J, Gao J-H, Lancaster J, Fox PT (1996) Assessment and optimization of functional MRI analyses. Hum Brain Mapp 4:153–167.

Young JP, Herath P, Eickhoff S, Choi J, Grefkes C, Zilles K, Roland PE (2004) Somatotopy and attentional modulation of the human parietal and opercular regions. J Neurosci 24:5391–5399.