cortex 64 (2015) 102–114

Available online at www.sciencedirect.com

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Research Report

Brain activity during observation and motor imagery of different balance tasks: An fMRI study

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ARTICLE INFO

Article history:
Received 27 March 2014
Reviewed 22 June 2014
Revised 14 August 2014
Accepted 30 September 2014
Action editor Georg Goldenberg
Published online 27 October 2014

Keywords:
Functional magnetic resonance imaging
Action observation
Motor imagery during action observation
Non-physical balance training

ABSTRACT

After immobilization, patients show impaired postural control and increased risk of falling. Therefore, loss of balance control should already be counteracted during immobilization. Previously, studies have demonstrated that both motor imagery (MI) and action observation (AO) can improve motor performance. The current study elaborated how the brain is activated during imagination and observation of different postural tasks to provide recommendations about the conception of non-physical balance training. For this purpose, participants were tested in a within-subject design in an fMRI-scanner in three different conditions: (a) AO + MI, (b) AO, and (c) MI. In (a) participants were instructed to imagine themselves as the person pictured in the video whereas in (b) they were instructed simply to watch the video. In (c) subjects closed their eyes and kinesthetically imagined the task displayed in the video. Two tasks were evaluated in each condition: (i) static standing balance and (ii) dynamic standing balance (medio-lateral perturbation). In all conditions the start of a new trial was indicated every 2 sec by a sound.

During AO + MI of the dynamic task, participants activated motor centers including the putamen, cerebellum, supplementary motor area, premotor cortices (PMv/d) and primary motor cortex (M1). MI showed a similar pattern but no activity in M1 and PMv/d. In the SMA and cerebellum, activity was generally higher in the dynamic than in the static condition. AO did not significantly activate any of these brain areas.

Our results showed that (I) mainly AO + MI, but also MI, activate brain regions important for balance control; (II) participants display higher levels of brain activation in the more demanding balance task; (III) there is a significant difference between AO + MI and AO. Consequently, best training effects should be expected when participants apply MI during AO (AO + MI) of challenging postural tasks.

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http://dx.doi.org/10.1016/j.cortex.2014.09.022

1. Introduction

After several days of involuntary immobility patients show impaired postural control and increased risk of falling (Visschedijk, Achterberg, van Balen, & Hertogh, 2010). It is therefore important to take steps to counteract loss of postural control during the period of immobility. Motor imagery (MI) of balance tasks has been shown to improve static postural control in elderly people (Hamel & Lajoie, 2005). Similarly, action observation (AO) was shown to improve performance in a sitting-to-standing-to-sitting task and in walking (Tia et al., 2010). These findings provide evidence that both MI and AO can improve postural control, but the neural sites responsible for this improvement have not so far been identified.

It is commonly agreed that the positive effects of MI and AO on physical task performance are probably explained by activation of overlapping brain areas during motor execution and MI as well as during motor execution and AO (Grezes, Armony, Rowe, & Passingham, 2003; Jeannerod, 1995, 2001; Olsson, Jonsson, & Nyberg, 2008). Jeannerod postulated the well accepted hypothesis that "the motor system is part of a simulation network that is activated under a variety of conditions in relation to action, either self-intended or observed from other individuals" (Jeannerod, 2001). This simulation network may differently be activated by different covert actions such as MI or AO although Jeannerod assumed a core network that pertains to all stimulation states (Jeannerod, 2001).

Previous studies investigating actual execution of postural tasks with neurophysiological (Beck et al., 2007; Schubert et al., 2008; Taube et al., 2007, 2006) and imaging methods (Ouchi, Okada, Yoshikawa, Nobezawa, & Futatsubashi, 1999; Taubert et al., 2010; Taubert, Lohmann, et al., 2011; Taubert, Villringer, et al., 2011) concluded that primary motor cortex (M1), visual cortex, the anterior and posterior cerebellar lobes, the basal ganglia (especially the putamen) and the brainstem are all involved in balance control in humans. Studies have also shown that physical execution of more demanding postural tasks was associated with higher activity in the supraspinal centers associated with postural control such as the cerebellum, the putamen, the brainstem and various neocortical structures (Ouchi et al., 1999). However, brain activity during MI and AO of balance tasks is rarely known. Jahn et al., (2004) used functional magnetic resonance imaging (fMRI) to demonstrate that activity of the thalamus, basal ganglia (left putamen), left frontal gyrus and spinocerebellum (cerebellar vermis) was increased when participants imagined they were standing rather than lying down. Furthermore, the pattern of activity during imagined standing was different from the pattern of activity obtained during imagined walking and running, in which a six times larger activity of the cerebellum could be detected. The authors therefore concluded that control of an undisturbed upright stance involves low intensity cerebellar activity and sensorimotor control via the thalamus and basal ganglia (Jahn et al., 2004). However, so far no previous study has investigated brain activity during MI or AO of balance tasks which require participants to counteract external perturbation.

Therefore, the first aim of the current study was to compare brain activity during a dynamic balance task (mediolateral perturbation) with activity in a less demanding static balance task (maintaining an upright stance). It is well known from non-postural tasks that MI (Gerardin et al., 2000; Grezes & Decety, 2001; Hallett, Fieldman, Cohen, Sadato, & Pascual-Leone, 1994; Jeannerod, 2001; Kimberley et al., 2006; Lotze et al., 1999; Sirigu et al., 1995; Stephan et al., 1995) and AO (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Grezes & Decety, 2001; Neuper, Scherer, Reiner, & Pfurtscheller, 2005) activate brain regions that are also active during actual task execution. Ouchi et al., (1999) have further demonstrated that execution of more challenging standing tasks increased brain activity; we therefore hypothesized that activity in motor centers would be higher in the more demanding dynamic task than during static standing.

The second main aim of the current study was to explore differences in brain activity according to the way participants mentally involved in the balance task. In a recent review article, Vogt, Rienzo, Collet, Collins, and Guillot (2013) have pointed out that MI and AO have been largely studied in isolation from each other but that combining both seems very promising. This statement was based on studies using electroencephalography (Berends, Wolkorte, Ijzerman, & van Putten, 2013) and fMRI (Macuga & Frey, 2012; Nedelko, Hassa, Hamzei, Schoenfeld, & Dettmers, 2012; Villiger et al., 2013; Vogt et al., 2013) to demonstrate higher brain activity during AO + MI compared with AO and MI, respectively, in non-postural tasks. In order to clarify whether this phenomenon can also be applied to balance tasks, differences in neural activation between a) 'motor imagery' (MI), b) 'actively' (AO + MI) and c) 'passively' (AO alone) observed balance tasks were investigated by instructing participants either to a) imagine the balance task (MI), b) imagine themselves as the person displayed in the video (AO + MI) or c) simply to watch the video (AO). In analogy to observations in voluntary hand movements (Berends et al., 2013; Macuga & Frey, 2012; Nedelko et al., 2012) we expected the activity to be greater during AO + MI than during AO or MI in both the static and dynamic balance task.

In summary, the overall goal of this study was to identify differences in the pattern of neural activity evoked by MI, AO and AO + MI of differently demanding balance tasks that can be used to develop recommendations for the non-physical training of immobilized patients.

2. Materials and methods

2.1. *Study participants*

Sixteen healthy participants (6 females) aged between 20 and 37 years (mean ± SD = 27 ± 4.81) free from neurological and orthopedic disorders participated in this study. They had normal or corrected-to-normal vision. All participants were briefed on the experiments and gave written informed consent to the experimental procedure before testing. The study was approved by the local ethics committee and was in accordance with the Declaration of Helsinki.

2.2. Experimental paradigm, stimuli and procedure

Participants were familiarized with the experimental conditions before scanning started: they watched a video showing the procedure and the various different tasks. After this familiarization phase participants entered the scanner for data acquisition. In the scanner, a video provided written and auditory information about which of the three conditions and which of the two tasks was about to be presented: The conditions (a) MI during AO (AO + MI), (b) MI, or (c) AO were tested in this order in separate runs with 3 min break in-between. In a random order, two videos showing two different motor tasks were displayed: (i) dynamic standing balance (medio-lateral perturbation on a laterally tilting surface) and (ii) static standing balance. The perturbation video showed a subject counteracting a medio-lateral perturbation in order to regain his balance. The standing video displayed a character in normal upright bipedal stance, thus hardly moving at all (see Fig. 1). Both videos were repeated every 2 sec for 10 times. Auditory and written instruction before each video provided information about what motor task was about to follow. Each experimental run was composed of 8 blocs (four dynamic and four static trials) and lasted 6 min. Each bloc was composed of a video which lasted 20 sec followed by a 21-sec rest period where a white cross on a black screen was displayed. On the video the start of a new trial was indicated every 2 sec by a sound (for both dynamic and static task). The order of presentation of the static and dynamic balance tasks was fully randomized within an experimental run. The MRI session lasted about 30 min.

During MI (a), participants were asked to imagine themselves performing either (i) the dynamic balance task (counteracting the perturbations of a wobble-board) or (ii) the static standing balance task on solid ground. During MI, a black screen was presented instead of animated videos. Auditory cues indicated the start of a new trial (every 2 sec). In addition, participants were asked to close their eyes during MI. They were instructed to focus their attention on their body and to imagine moving specific body parts as required by the task. In other words participants were instructed to use first-person 'kinesthetic imagery'. In the AO + MI (b) and AO (c) conditions participants watched a video displaying a person performing either the dynamic balance (i) or the static balance (ii) task (Fig. 1). In the AO + MI condition (b), participants were instructed to imagine themselves as the person in the video displayed in a mirror whereas in AO (c) they were instructed simply to watch the video. The person in the video was displayed as a mirror image because it has been proposed that imitation (Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003) and observational learning (Higuchi, Holle, Roberts, Eickhoff, & Vogt, 2012) are facilitated by this kind of setup.

2.3. Experimental material

Participants assumed a supine position on the scanner bed and cushions were used to reduce head motion. Visual stimuli were presented on an LCD screen (32″ NNL LCD Monitor, NordicNeuoLab, Bergen, Norway) with E-Prime 2.0 software (Psychology Software Tools, Inc., www.pstnet.com, PA, USA) at 60 Hz. Participants looked at the screen through a mirror system.

The videos were presented with at a visual angle of 17° (vertical plane) and 9° (horizontal plane).

2.4. Image acquisition

The experiments were conducted using a 3T MRI scanner (Discovery MR750; GE Healthcare, Waukesha, Wisconsin USA)

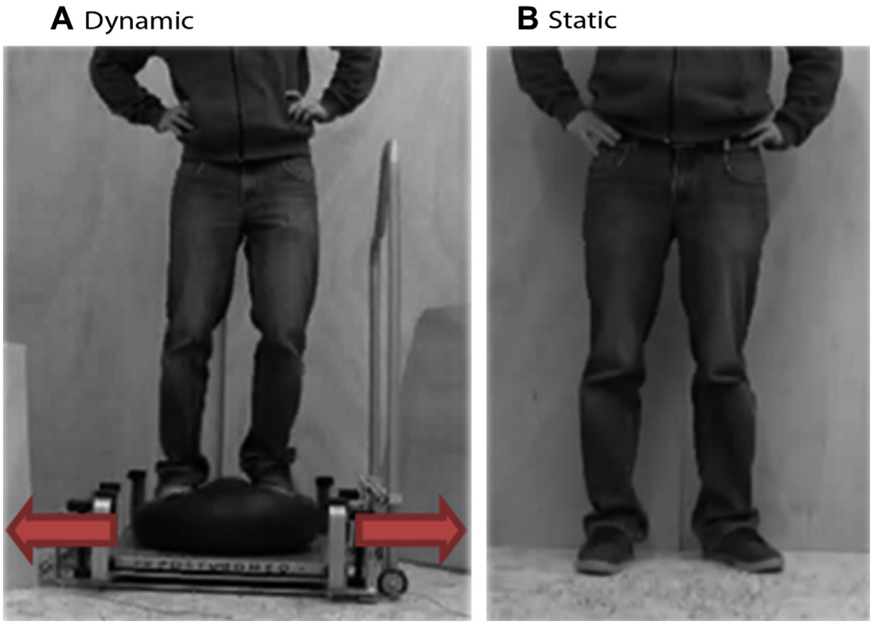

Fig. 1 – Illustration of the balance tasks shown in the videos during the experimental procedure. (A) In the dynamic balance task ('perturbation') the video showed a person compensating for the lateral tilting of a wobble-board. (B) In the static balance task the same person was shown standing upright, in a relatively static pose with only subtle body sway. Participants were asked to observe these videos as looking into a mirror.

at the Fribourg hospital in Switzerland (www.h-fr.ch/). A 32-channel standard head coil was used for acquisition. High resolution T1-weighted anatomical scans were recorded in the coronal plane in an anterior direction (FSPGR BRAVO sequence; voxel size = .86 × .86 × 1 mm, number of slices = 220, repetition time (TR) = 7200 msec, echo time (TE) = 2.4 msec, flip angle = 9°). Functional T2*-weighted images were acquired using a Gradient Echo–Echo Planar Imaging (GE-EPI) sequence. The blood oxygenation level-dependent contrast (BOLD) (Kwong et al., 1992) was used as an index of local increases in brain activity. 140 dynamic volumes with axial acquisitions were recorded over the whole brain (voxel size = 1.875 × 1.875 × 3 mm, matrix size = 128 × 128, number of slices = 40; interleaved acquisition from the bottom to the top of the head, interslice spacing = .3, TR = 2500 msec, TE = 30 msec, flip angle = 85°; parallel imaging with an acceleration factor of 2) for each experimental session. In each run functional scanning was preceded by 7.5 sec of dummy scans to ensure steady-state tissue magnetization.

2.5. *Data analysis*

MRI data were analyzed with the Statistical Parametric Mapping SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/) working on Matlab 2010b (MathWorks, Inc., http://www.mathworks.com, MA, USA). All functional volumes were subjected to standard preprocessing procedures (Friston, Ashburner, Kiebel, & Penny, 2007), including spatial realignment, co-registration with the anatomical scan, normalization [on the Montreal Neurological Institute (MNI) space with $2 \times 2 \times 2$ mm^3 voxels] using the unified segmentation of the anatomical scan and smoothed with an isotropic 6 mm full width half-maximum (FWHM) Gaussian kernel. Time series from each voxel were high-pass filtered (1/128 Hz cutoff) and the preprocessed functional volumes were then submitted to fixed-effects analysis (i.e., first level analysis, FFX) using a block design, applying the general linear model to each voxel (Friston et al., 1995; Worsley & Friston, 1995) and using an auto-regressive [AR(1)] function to account for temporal correlations between voxels across the whole brain. Afterwards, the data were submitted to second-level analysis (random effect analysis, RFX) in order to generalize the results for the population. All conditions were modeled in a full factorial model (ANOVAs) 3 × 2 (F1: condition; F2: task). The coordinates derived from these analyses (cluster maxima) were converted from MNI coordinates to Talairach and Tournoux stereotaxic coordinates using the *icbm2tal* script (Lancaster et al., 2007) in order to associate the results with an anatomical location (Talairach & Tournoux, 1988). The WFU pickAtlas software (Maldjian, Laurienti, & Burdette, 2004; Maldjian, Laurienti, Kraft, & Burdette, 2003) was used to define anatomical locations based on the Talairach Daemon atlas database (Lancaster et al., 2000) and the automatic anatomical labeling (AAL) tool (Tzourio-Mazoyer et al., 2002). Anatomical labels were assigned according to the nearest gray matter position. All illustrations are based on this neurological convention.

Statistical parametric maps (SPMs) were assessed to determine the brain activation associated with each experimental context (simple effects). Effects were recognized at $p < .05$ corrected for multiple comparisons at the voxel level (FWE). SPMs were also computed to compare brain activity across tasks in the active condition (dynamic *vs* static) as well as between AO + MI and AO in the dynamic task. Significant differences were recognized at $p < .001$, uncorrected at the voxel level but with an extended cluster threshold of 240 contiguous voxels ($p_{cluster} < .05$; false discovery rate (FDR) corrected) for topological analysis (Chumbley & Friston, 2009). In this manuscript, all locations are presented in MNI coordinates (*x*, *y*, *z*) and the Tables provide details of the local maxima for each cluster.

In the first part of this study, the pattern of brain activation in each experimental task was studied with simple effect comparisons (contrast between task and resting state). In order to assess differences in brain activity due to changes in the complexity of the balance task, direct comparisons between dynamic and static balance tasks were performed for the AO + MI and AO conditions and the MI condition. Differences between the pattern of activation in AO + MI and AO were assessed comparing activity in both tasks (dynamic and static balance). Brain activity during AO + MI was also compared with the brain activity during MI and the contrast between MI and AO was analyzed, too. We also conducted a conjunction analysis ($p < .05$, FWE corrected) to identify brain areas recruited during both MI and AO + MI of movement. Further, to test whether MI during AO (AO + MI) is simply the sum of brain activity observed during AO and MI, a contrast was calculated for AO + MI versus the summed activity of AO and MI. Finally, we conducted a region of interest (ROI) analysis on M1 (identified according to the Brodmann area 4 of the Talairach Daemon atlas based on the WFU PickAtlas software to generate ROI masks). The ROI was applied as an explicit mask on the model and results were analyzed with a $p < .05$ FWE corrected statistic for multiple comparison at the voxel level.

3. Results

3.1. *Simple effects*

3.1.1. *Activity in SMA, premotor cortex, M1, putamen, and cerebellum*

The activation maps in Fig. 2 illustrate the pattern of activation associated with each experimental condition in comparison with the resting state (for parameter estimates see Fig. 6 in the supplementary material). Bilateral activity in the SMA, putamen and cerebellum was detected in the MI condition (Fig. 2A). AO + MI also activated the SMA, putamen and cerebellum and there were additional activation foci in ventral premotor cortex (PMv) and dorsal premotor cortex (PMd) (Fig. 2B). Furthermore, the ROI analysis on M1 revealed significant activity on the left side during AO + MI of the dynamic task ($p < .001$). Interestingly, no significant activity was detected in the SMA, premotor cortices, M1, basal ganglia or cerebellum during AO (Fig. 2C).

3.1.2. *Activity in other brain regions*

Bilateral activity in the superior temporal gyrus (STG; BA 41, 42), which corresponds to the location of the primary auditory cortex, was detected in all the experimental conditions. In

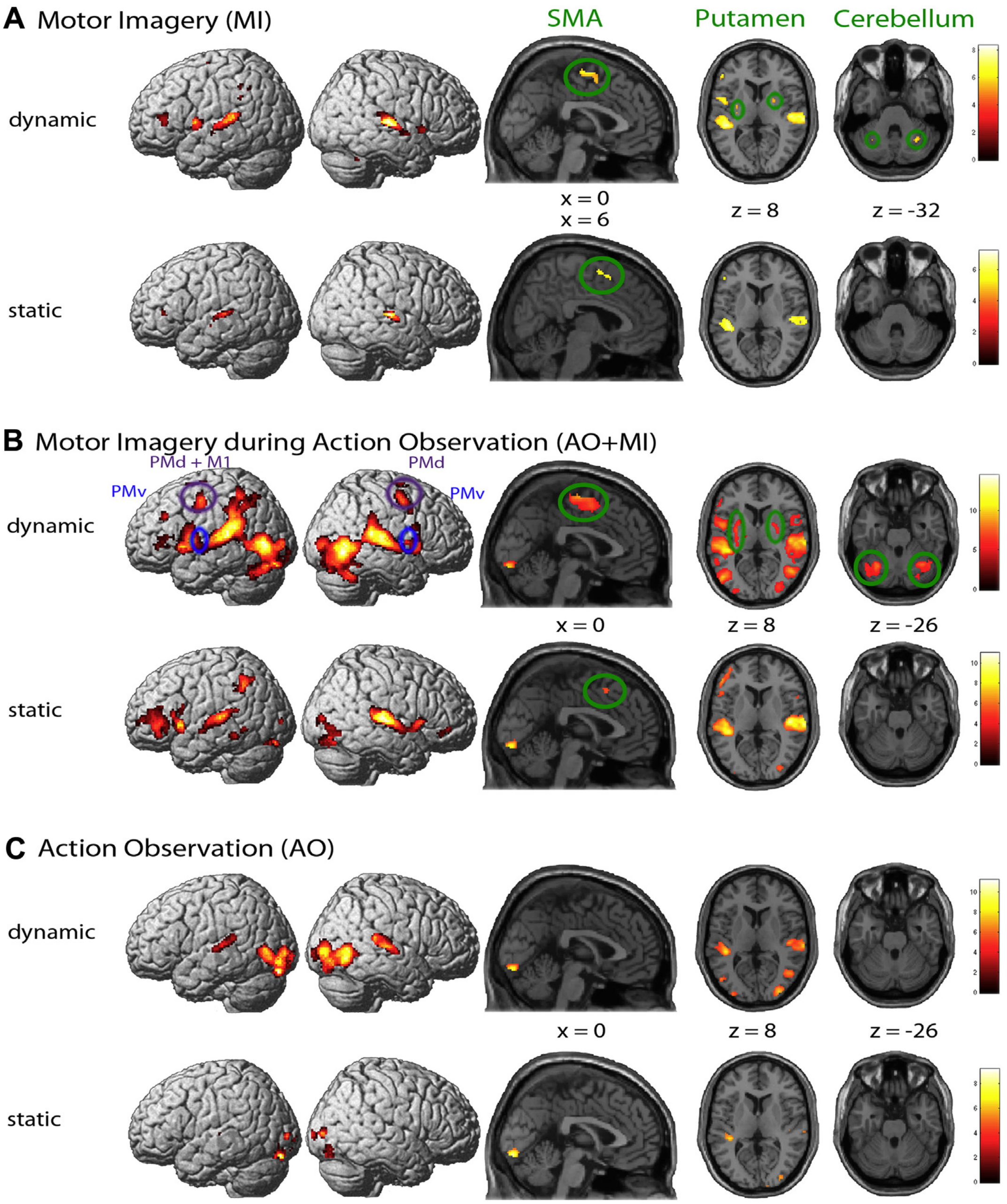

Fig. 2 – Brain activity associated with each experimental condition. (A) shows the results of MI of the 2 movements (dynamic and static). (B) shows the pattern of brain activation when participants applied MI during AO (AO + MI) and (C) shows the results of AO (AO for the 2 tasks.. In the three columns on the right significant activity in the SMA, putamen, and cerebellum is marked with a green circle. It can be seen that these structures are activated during MI and AO + MI and that this activation is larger in the dynamic (perturbation) than in the static (standing) task. AO + MI additionally activates ventral premotor cortex (PMv; in blue) and dorsal premotor cortex (PMd; in purple) as well as the primary motor cortex (M1; in purple) Activations are displayed with $p < .05$ FWE corrected statistics at the voxel level. Color bars show the significance level of each experimental condition. The coordinates (*x*, *z*) of each section in MNI space are provided.

addition, a specific region of the STG, corresponding to BA 22, was consistently activated across conditions.

The visual cortex (BA 17, 18, 19) was strongly recruited during AO + MI and AO but not during MI – participants were asked to close their eyes in this condition. The inferior frontal gyrus (BA 44, 45, 46) was activated bilaterally, with left hemisphere dominance, during AO + MI. This region was also active during MI of the balance task (BA 46, left hemisphere only). The insula (BA 13) showed bilateral activation during AO + MI or MI of the dynamic balance task. Activity was detected in the right insula during AO of the dynamic task but at a much weaker intensity than in the AO condition.

3.2. *Comparisons of conditions and tasks*

3.2.1. *Dynamic versus static balance tasks across conditions*

In order to investigate whether the complexity of the balance task had an influence on activation of brain centers associated with balance control, the dynamic balance task was contrasted with the static balance task. During AO + MI, this comparison revealed significantly higher activity in the SMA and cerebellum (Fig. 3A). Additional regions, namely the left inferior occipital gyrus (BA 19), right middle temporal/fusiform gyrus (BA 37) and the bilateral superior and left superior temporal gyrus (BA 20, 41, 42), were more strongly activated in the dynamic task (for details see Table 1A). During AO, no differences between activity in the dynamic and static tasks were detected in the SMA, basal ganglia or cerebellum (Fig. 3B); however, significant task difference for other brain regions were evident in AO (see Table 1B). No significant differences between activity on the dynamic and static tasks were seen in the MI condition, although simple effects analysis indicated that the SMA and cerebellum were more strongly activated in the dynamic task (Fig. 2).

3.2.2. *AO + MI versus AO*

AO + MI of the dynamic task resulted in greater activity in SMA, basal ganglia (putamen and caudate), and cerebellum than AO (contrast: AO + MI > AO) (Fig. 4). In addition, during AO + MI there was significant activity in the precentral gyrus, particularly in PMv, but also in PMd. In both regions activation was more pronounced in the left hemisphere. The ROI analysis for M1 showed greater activity on the left side during AO + MI than during AO ($p = .045$). Several other regions including the left superior and right inferior frontal gyrus (BA 9), the inferior parietal lobule (BA 40), insula (BA 13) and thalamus, displayed greater activity during AO + MI than AO (for details see Table 2). Similar, but weaker effects were found for AO + MI versus AO of the static task: the SMA, basal ganglia, right cerebellum and premotor cortices (PMv and PMd) were more strongly activated during AO + MI than AO (not illustrated due to space limitations). For the inverse contrasts (AO *vs* AO + MI; dynamic and static), there were no significant findings.

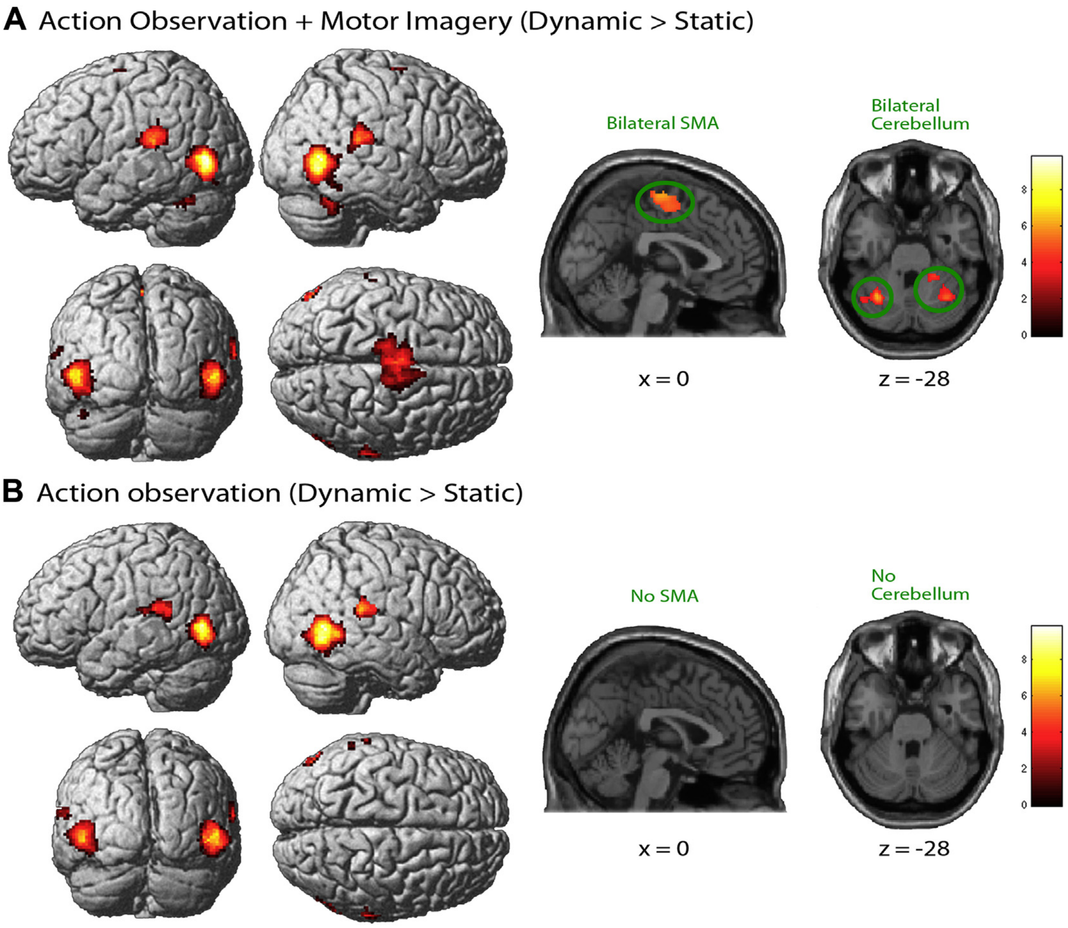

Fig. 3 – Contrasts in brain activity between the dynamic (perturbation) and static balance (standing) condition for AO + MI (A) and AO (B). The two columns on the right show that bilateral SMA and cerebellum display significant differences for AO + MI but not for AO. Activations are displayed with $p < .001$ uncorrected statistics with an extended cluster threshold of 240 contiguous voxels. Color bars show the significance level of each contrast. The coordinates (*x*, *z*) of each section in MNI space are provided. Activation details can be found in Table 1.

Table 1 – Comparison of the dynamic balance task with the static balance task during combination of AO and MI (AO + MI; see A) and AO (AO; see B). Each table is split in 3 parts: left, right and bilateral activations. The cluster size column gives the number of voxel present in each activation cluster. The spatial location (coordinates) of voxels with the highest Z-score (Z-max) inside of each cluster is displayed. Associated activations are shown in Fig. 3.

Anatomical location	BA	Coordinates (x, y, z)			Cluster size	Z-max
A. AO + MI (Dynamic > Static task)						
Left superior temporal gyrus	22/40/41	−46	−34	18	592	4.94
		−58	−38	16		4.12
		−46	−38	32		3.12
Left inferior occipital gyrus	19	−40	−72	2	1030	7.46
		−46	−80	−14		3.18
Left cerebellum (culmen/tuber)		−30	−58	−28	222	5.6
		−44	−62	−28		3.51
Right middle temporal/fusiform gyrus	37	48	−64	−2	1316	>7.84
		42	−46	−16		4.77
Right insula	13	52	−36	16	490	4.97
Right superior temporal gyrus	41/42	66	−26	16		4.18
Right cerebellum (culmen/tonsil)		34	−60	−28	291	4.71
		34	−52	−36		4.61
		24	−40	−28		4.17
Medial frontal gyrus – both hemispheres (SMA)	6	−4	−10	62	1060	4.9
		−2	−18	62		4.88
		12	−20	66		4.72
B. AO (Dynamic > Static task)						
Left middle temporal gyrus	22	−48	−44	14	388	4.32
Left superior temporal gyrus	22/40/41	−60	−46	18		3.72
		−54	−28	14		3.39
		−62	−24	16		3.22
Left insula	13	−48	−40	18		4.13
Left inferior occipital gyrus	19	−42	−72	2	858	6.93
Right middle temporal/fusiform gyrus	37	48	−62	0	1713	7.81
		46	−60	−16		3.26
Right superior temporal gyrus	41	44	−36	10		3.37
right insula	13	60	−34	18		4.98

3.2.3. *AO + MI versus MI*

The contrast between AO + MI and MI (AO + MI > MI) on the dynamic task revealed greater bilateral activity in the cerebellum during AO + MI (Fig. 5). The ROI analysis for M1 showed greater bilateral activity during AO + MI than MI ($p = .004$ for the right and $p = .016$ for the left). In addition, visual centers such as the inferior and middle occipital gyrus (BA 18, 19) and fusiform gyrus (BA 19, 37) were recruited during AO + MI. Furthermore, the precuneus showed greater activation during the AO + MI condition than the MI condition.

On the static balance task, the same comparison shows that cerebellar activity was again more pronounced in the

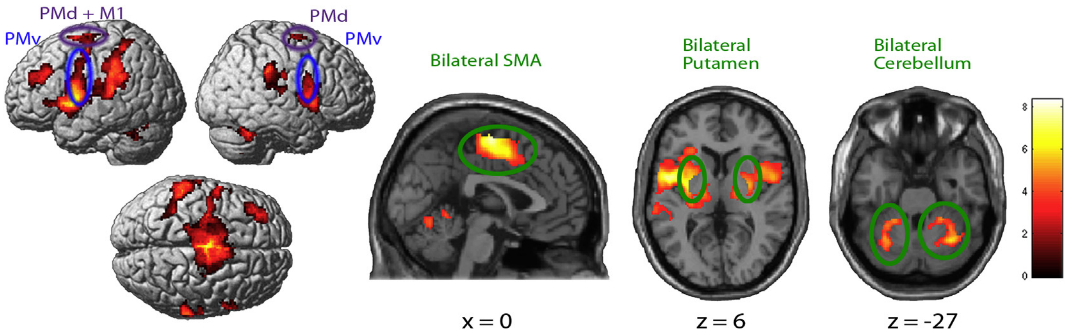

Fig. 4 – Contrast in brain activity between AO + MI and AO of the dynamic balance task. Colored circles highlight the structures that are more involved in AO + MI than AO; PMv = ventral premotor cortex, PMd = dorsal premotor cortex, M1 = primary motor cortex. Activations are displayed with $p < .001$ uncorrected statistics with an extended cluster threshold of 240 contiguous voxels. Color bars show the significance level of the contrast. Numbers behind sections indicate their localization in MNI space. Activation details can be found in Table 2.

Table 2 – Comparison between the combination of AO and MI (AO + MI) and AO during the dynamic balance task. The table is split in 2 parts: left and right activations.

Anatomical location	BA	Coordinates (x y z)			Voxel amount	Z-max
Left medial frontal gyrus (SMA)	6	−4	−10	60	665(^{*1})	7.15
	6	−12	−20	64		4.79
Left precentral gyrus	4	−26	−16	56	1203(^{*1})	4.49
	44	−50	0	6		6.6
Left superior frontal gyrus	9	−30	40	26	69(^{*1})	4.51
Left inferior parietal lobule	40	−58	−38	28	728(^{*1})	4.74
Left insula	13	−34	28	2	891(^{*1})	4.55
Left caudate tail		−20	−28	18	7(^{*1})	4.51
Left putamen		−20	0	14	413(^{*1})	5.01
Left thalamus		−16	−14	6	373(^{*1})	4.5
Left cerebellum		−32	−56	−30	525	4.73
Left cerebellum (tonsil)		−30	−56	−36		4.61
Left cerebellum (culmen)		−10	−52	−16		4.19
Right medial frontal gyrus (SMA)	6	4	−10	64	740(^{*1})	6.21
	6	2	−14	60		6.07
Right superior temporal gyrus	42	68	−30	18	548	3.67
	22	68	−34	16		3.63
Right inferior parietal lobule	40	64	−32	30		4.67
Right precentral gyrus	44	52	2	6	1856	4.89
Right inferior frontal gyrus	9	56	6	22		4.21
Right insula	13	44	10	2		4.77
Right caudate body		20	14	10		3.45
Right putamen		28	−6	8		4.98
Right thalamus		18	−16	8		4.65
Right cerebellum (tonsil)		34	−50	−36	608	6.15
Right cerebellum (culmen)		34	−42	−30		4.63
Right cerebellum (uvula)		14	−46	−26		3.38

^{*1}indicates that these regions belong to the same cluster but the voxel amount is split according to the definition of the anatomical structure in the Talairach atlas (regions were selected according to the localization of the local maxima). The spatial location (coordinates) of voxels with the highest Z-score (Z-max) inside of each cluster is displayed. Associated activations are shown in Fig. 4.

AO + MI condition than in the MI condition (not illustrated due to space limitations). Finally, the inverse contrasts (MI > AO) did not show significant differences for dynamic and static task, respectively.

3.2.4. *MI versus AO*

A comparison between brain activity in the MI and AO conditions (MI > AO) during the dynamic task revealed greater activity in the SMA, left precentral gyrus (BA 44), right insula (BA 13), left middle frontal gyrus (BA 9), and left thalamus. Activity during the static task for the MI > AO contrast showed a similar pattern, although there was no difference between the conditions for the right insula (not illustrated due to space limitations). The inverse contrast PO > MI showed mainly activation in visual cortices of the bilateral occipital lobe with a supplementary activity in the right lateral geniculum body (not illustrated due to space limitations).

3.2.5. *AO + MI compared with the additive combination of MI and AO*

Brain activity during MI of the observed movement (AO + MI) did not correspond simply to the sum of activation in the MI and AO conditions; activity in the bilateral cerebellum as well as bilateral precuneus (Brodman area 7) and left posterior cingulate/cuneus (Brodmann area 30) was significantly higher than the sum of brain activity during AO and MI. Furthermore, the ROI analysis on M1 revealed significantly greater right sided activity in the AO + MI condition than when summing up activities of MI and AO ($p = .022$).

3.2.6. *Overlapping brain areas are activated during AO + MI and MI*

The conjunction analysis revealed that AO + MI and MI of the dynamic task activated an overlapping motor network consisting of the SMA, cerebellum and putamen as well as the superior temporal area responsible for auditory processing (see Fig. 7 in the supplementary material).

4. Discussion

The results of this study demonstrated that during AO + MI and MI the brain areas most consistently activated were the cerebellum, the putamen and the SMA. Activation in these areas was generally higher for the dynamic balance task than the static balance task. AO + MI additionally activated premotor cortex (PMv and PMd) and the primary motor cortex (M1). AO of balance tasks did not result in significant activation of the cerebellum, putamen, SMA, M1 or premotor cortices.

Our results demonstrate that (I) primarily AO + MI but also MI activate brain regions known to be important for balance control; (II) brain activation is more widespread and intense in the more demanding balance task and (III) AO does not induce

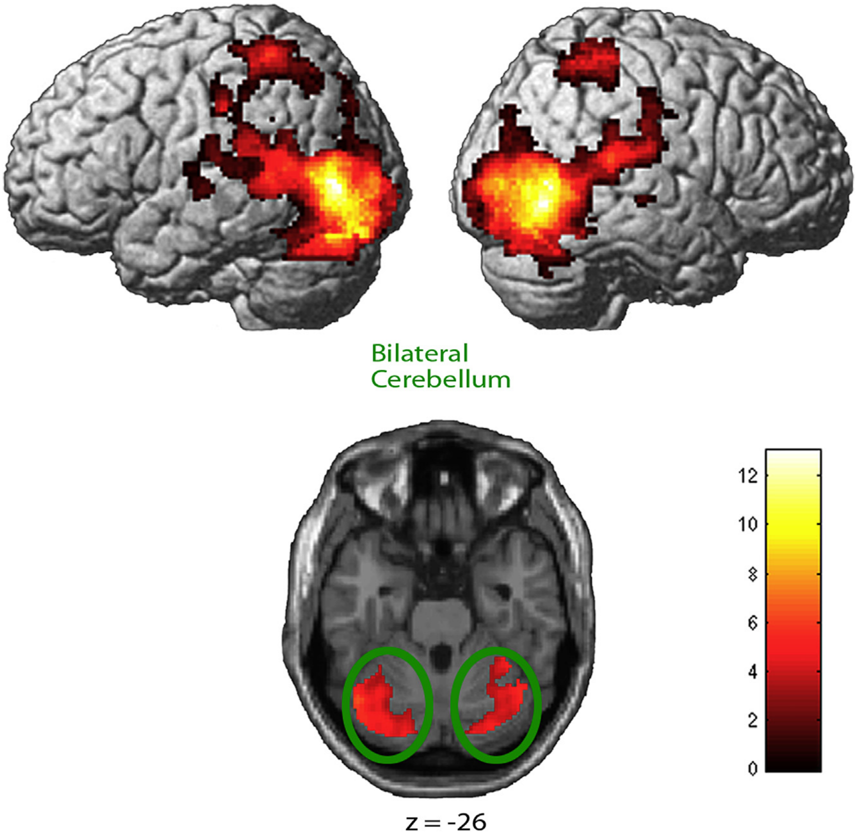

Fig. 5 – Contrast in brain activity during AO + MI and MI of the dynamic balance task. The colored circle highlights that the bilateral cerebellum is more involved in AO + MI than MI. Activations are displayed with $p < .001$ uncorrected statistic with an extended cluster threshold of 240 contiguous voxels. Color bars show the significance level of the contrast. The number behind the section indicates its localization in the MNI space.

detectable activity in the brain areas responsible for balance control. These results suggest that the most effective form of non-physical training would involve AO + MI of demanding balance tasks followed by MI of such tasks; AO is not likely to be effective as it does not appear to produce sufficient activation of the relevant brain centers.

4.1. *The influence of task difficulty: comparison of the static and dynamic balance tasks*

Overall, brain activity was higher in the more difficult dynamic balance task than the static balance task (Fig. 2). There was differential activation of brain areas that are thought to be especially relevant to postural control; in particular there was greater activation of the SMA and cerebellum during AO + MI (Fig. 3). There were no significant task differences in activation of these regions in the AO and MI conditions, although simple effect analysis indicated stronger activation of SMA and cerebellum in the dynamic balance task, which required continual postural adjustment (Fig. 2).

These findings are in line with previous observations (Jahn et al., 2004; Ouchi et al., 1999). Ouchi et al. (1999) did not investigate dynamic balance tasks, but using position emission tomography (PET), they nevertheless neatly demonstrated that increasing the postural demands of static tasks (standing, standing with feet together, standing in tandem stance) resulted in an increase in cerebellar activity. Similarly, using fMRI Slobounov, Wu, and Hallett (2006) showed increased activity in several brain areas including the cerebellum, basal ganglia (putamen and caudate nucleus), parietal cortex and anterior cingulate cortex whilst participants were observing a computer-animated body model in unstable – i.e., more demanding – postures than when observing the same model in a stable posture. Interestingly, participants who were unable to detect instability in the animated model showed postural instability when performing a balance task. The results of this study suggested that brain activity during AO of postural tasks was indicative for the ability to control upright stance.

4.2. *The influence of mental involvement: comparison of MI, AO and the combination of both*

There have been several studies comparing the effects of imagined and observed tasks. The results are inconsistent. For instance, Szameitat, Shen, Conforto, and Sterr (2012) compared patterns of brain activation during execution, passive movement, MI and AO of flexion–extension movements of the wrist. In healthy participants, the condition which produced the pattern of activity most closely resembling that seen during task execution was passive movement, followed by MI, then AO. In stroke patients, MI produced the pattern of activity which most closely resembled that seen during task execution, followed by passive movement, then AO. The authors concluded that MI would have training effects superior to those of movement observation in both healthy participants and hemiparetic stroke patients. In contrast, Gatti et al. (2013) observed better performance on a novel, complex motor task after observational learning than MI. Therefore, although it is well established that both MI and AO of movement can be used to facilitate motor learning, it is not currently possible to conclude that one form of training is more effective than the other. Many factors, such as task difficulty, task novelty, the general motor experience of the learner, individual differences in motor learning style (e.g., 'visual type' *vs* 'mental type'), and the form of instruction may influence the outcome of training. It was for instance shown that participants who were asked to watch a movement in order to imitate this movement later on (called 'active observation') showed greater corticospinal excitability than the same participants watching the movement 'passively' without this instruction (Roosink & Zijdewind, 2010). This indicates that it matters how movements are observed. In line with this assumption, recent fMRI studies investigating non-postural tasks demonstrated greater brain activity when MI was simultaneously performed during AO (AO + MI) than applying AO or MI alone (Berends et al., 2013; Macuga & Frey, 2012; Nedelko et al., 2012; Villiger et al., 2013; Vogt et al., 2013). The current results further strengthen and extend this picture to balance tasks. The highest and most widespread levels of activity in motor related areas (M1, PMv & PMd, SMA, cerebellum, putamen) occurred during AO + MI, followed by MI, then AO. Conjunction analysis revealed largely overlapping patterns of activity in motor centers (SMA, cerebellum and putamen) when comparing the AO + MI and MI in the dynamic task. Interestingly, brain activity in the cerebellum, the precuneus, the posterior cingulate/cuneus and the primary motor cortex during AO + MI was not simply the sum of activity of AO and MI; it was significantly higher than the sum of these two conditions. This suggests that MI during AO (AO + MI) evokes a supra-summative brain activity that cannot be obtained by simply adding activities from MI and AO. It is therefore assumed that AO + MI should be the most effective form of non-physical balance training.

Surprisingly, AO did not result in any significant activity of motor centers at all. This is in contrast to previous studies investigating brain activity during the observation of goal-directed movements of the upper extremity. In these studies activity in the premotor cortex, the primary motor cortex, the SMA, and the cerebellum was reported (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes et al., 2003; Hari et al., 1998; Jeannerod, 2001). Consequently, it might be speculated that the brain is differently activated during observation of balance tasks than during observation of goal-directed movements of the upper extremity. This seems plausible as it was previously shown in a well-controlled study that corticospinal excitability was enhanced when observing transitive (i.e., goal-directed movements such as grasping a cup) but not when observing intransitive (i.e., movements not associated with a particular object or goal) hand gestures (Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2010). Thus, (the presented) balance tasks might in this sense be classified as intransitive movements consequently eliciting little brain activation when solely observing them without further mental effort. In any case, our results underline the importance of combining AO with MI (AO + MI) with respect to non-physical balance exercises as AO alone seems not appropriate to efficiently activate the relevant motor centers.

One limitation of the current study is that the conditions (AO + MI, MI, and AO) were not randomized. It might therefore be argued that carryover effects or fatigue could influence the different conditions in a different way. However, considerable carryover effects are unlikely as the activity was always larger in the first condition than in the following ones. Fatigue is also unlikely as participants had sufficient rest between conditions in which they could relax. Furthermore, as we used the same experimental paradigm, but this time with randomization of conditions, in elderly people and found very similar brain activation patterns (manuscript in preparation), we do not think that the order of conditions considerably influenced the general outcome. Another limitation is that we could not compare the pattern of activation during observation and MI with activity during performance of the same balance tasks as it is clearly impossible to monitor brain activity during balancing using fMRI. In consequence, in the following section only activation patterns during observation and imagination of movement are discussed with respect to their potential relevance to balance control.

4.3. *Are the patterns of activation observed in the present study relevant to balance control?*

La Fougère et al. (2010) showed that MI of upright locomotion induced activity in the SMA and the basal ganglia, whereas PET during real locomotion revealed strong foci of activation in the primary motor and somatosensory cortices. It may therefore be argued that the patterns of activity during MI and task execution may differ considerably, and specifically that activity of the SMA and basal ganglia might be exclusively associated with the cognitive demands of MI and AO + MI of movement rather than being associated with execution of balance tasks. However, several arguments can be made against this line of reasoning. Firstly, la Fougère et al. highlighted the differences between the tasks for MI of locomotion and execution of locomotion in their study: whilst the locomotor execution task was performed at the same velocity over a 10 min trial, the MI task involved short sequences of 20 sec walks and included gait initiation and changes in velocity. La Fougère et al. hypothesized that there might exist two pathways a 'direct pathway' via the primary motor cortex for steady-state locomotion and a more 'indirect pathway' via the SMA for imagined modulatory locomotion. Secondly, Taubert and colleagues demonstrated significant structural and functional adaptation of the SMA after balance training, and suggested that this indicated that the SMA plays an important role in the execution of demanding balance tasks (Taubert et al., 2010; Taubert, Lohmann, et al., 2011). Thirdly, PET scans during a task involving walking revealed additional engagement of the SMA when the task involved walking over obstacles rather than walking normally (Malouin, Richards, Jackson, Dumas, & Doyon, 2003). This implies that higher brain centers are recruited when the demands of a locomotor task are increased or task performance is less automatic. All these data obtained during or after execution of movement provide evidence that the SMA plays an important role in demanding balance tasks such as the dynamic balance task used in this study.

Similarly, there is widespread recognition that the basal ganglia are important for balance control, for instance they enable postural flexibility and sensorimotor integration (Visser & Bloem, 2005). Goble et al. (2011) used fMRI to record brain activation during 80 Hz vibration of the foot, a stimulus known to excite Ia afferents. The stronger the activity in the putamen and certain cortical areas (parietal, frontal, and insular cortical areas), the better participants performed during a task which required them to maintain an upright stance with their eyes closed; this suggests that activity of the basal ganglia, and more specifically the putamen, may be an index for the capacity for certain postural functions.

The enhanced activity in the premotor cortices during AO + MI of the dynamic balance task in this study may be related to its role in preparing anticipatory postural adjustments (Chang et al., 2010). Sensorimotor training induced larger increases in gray matter volume in PMd in patients with cerebellar degeneration than in healthy controls, whereas healthy controls showed more pronounced increases in the cerebellum (Burciu et al., 2013). In line with this finding, near-infrared spectroscopic imaging revealed involvement of the premotor cortex in the restoration of gait after stroke (Miyai et al., 2002). Taken together these results suggest that premotor cortex may be involved in learning balance tasks and this involvement may be particularly apparent when other structures normally involved in such tasks, e.g., the cerebellum, are impaired. Alternatively, the activity we observed in premotor cortex in this study could be explained in terms of understanding motor actions and related to functioning of the mirror neuron system (for review see Morin & Grezes, 2008). However, there is currently no data on activity of mirror neurons in balance tasks. Further studies should investigate potential similarities and differences between the whole body task of maintaining or regaining balance and goal-directed reaching movements of the arms, as premotor cortex has been shown to be activated during both execution and observation of goal-directed reaching.

The ROI analysis for M1 revealed significant activity during AO + MI of the dynamic task. However, neither MI nor AO elicited any activity in M1. This may surprise as there is evidence that M1 is not only involved in dynamic (Taube et al., 2006) but also static balance control (Tokuno, Taube, & Cresswell, 2009) and adapts in response to balance training (Beck et al., 2007; Schubert et al., 2008; Taube et al., 2007). The adaptations in M1 were thereby correlated to balance performance (Taube et al., 2007) indicating that this region is essential for balance control.

There was activity in the insula during AO + MI or MI of the dynamic balance task. The increased activation in the dynamic balance task may relate to its role in the vestibular cortical network involved in spatial orientation and self-motion perception (Lopez & Blanke, 2011; Ward, Brown, Thompson, & Frackowiak, 2003); there is a report of recurrent episodes of vertigo in a patient with a small lesion in the right insula (Papathanasiou et al., 2006). In addition, it has been suggested that the right insula plays a prominent role in the sense of 'limb ownership' and the feeling of being involved in a movement (Karnath & Baier, 2010). The right insula was not activated by AO; this may reflect a substantial difference between AO + MI and AO and suggests that AO alone is not sufficient to feel engaged in these balance tasks.

The bilateral inferior frontal gyrus (BA 44, 45, 46) was activated with a left hemisphere dominance during AO + MI of movement. Part of this region (left BA 46) was also active during MI of the dynamic balance task. It has been speculated that the Broca region (particularly BA 44) may form part of the mirror neuron system (Grezes et al., 2003), which may also be activated by observation and MI of movement (Gatti et al., 2013).

5. Conclusion

In summary, there is ample evidence that the SMA, premotor cortex, M1, basal ganglia (putamen), and cerebellum play a significant role in physically executed balance control (see section above). Now, the current study showed for the first time that these regions can also be activated by AO + MI of a dynamic balance task; MI produced comparable activity in the SMA, putamen and the cerebellum but non-significant activation of M1 and PMv/d. In contrast, AO did not activate any of these motor areas. Furthermore, for AO + MI and MI, activity was generally greater in the dynamic perturbation task compared to the static standing task. Based on these results it may be argued that best training effects should be expected when subjects apply MI during AO (AO + MI) of challenging balance tasks. This might be especially relevant for temporarily immobilized patients that want to reduce their risk of falling in the recovery phase after immobilization. However, future research in immobilized subjects has to verify that AO + MI indeed lead to faster regains in skill level.

Acknowledgement

This work was supported by the Swiss National Science Foundation (SNF research grant 320030_144016 / 1).

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.09.022.

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