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Awareness of the muscular forces we produce during voluntary movement must be distinguished from awareness of motor outcome itself. Indeed, there is no univocal relationship between produced muscle force and movement outcome because of external forces. In the present study, we performed a functional magnetic resonance imaging study to investigate the neural bases underlying the awareness we can have of the muscular forces we put into our voluntary movements. In reference conditions, subjects made rhythmical hand movements and knew they had to reproduce, in a subsequent condition in which the resistance to the movement was increased, either their muscular forces or their kinematics. The idea behind this (well established) reproduction paradigm is that, after an explicit verbal instruction, subjects can only reproduce what they are aware off. The main contrast, that is, between the condition during which the subjects had to gain awareness of their muscular forces and that during which they had to gain awareness of their kinematics (conditions in which the actual motor output was similar), shows that gaining awareness about muscular forces exerted during movement execution makes much higher demands on many brain structures, in particular posterior insula, primary sensorimotor areas and associative somatosensory areas. This indicates the important role of somesthetic information processing in awareness of produced muscular force. Therefore, the often-heard presumption that muscle force sense might be based on the outgoing motor command is not confirmed by the present results.
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Introduction

In motor control literature, motor awareness is often considered as explicit knowledge about our own motor output (Haggard et al., 2002; Tsakiris and Haggard, 2003). Since it is, by definition[1], an "inner subjective state" and thus not directly accessible by a third person, one means of studying this, among others, has been to ask subjects to accurately reproduce a movement immediately after its production (e.g., Fourneret and Jeannerod, 1998; Johnson et al., 2002). The basic assumption of such a reproduction paradigm is that the movement characteristics that we reproduce are those of which we are aware. Moreover, to reproduce a movement, a rough awareness is not sufficient, an awareness with a precise content is required. With such paradigm, it has been shown that we are not necessarily aware of all aspects of movement production.

In the same way, one could define muscle force awareness as explicit knowledge about the muscular force applied to produce our voluntary movement. This awareness of produced muscle force should be well differentiated from awareness of movement outcome, since no univocal relationship exists between muscle force production and movement outcome. Indeed, all biological movements are the result of the integration of two types of force: active and passive (Bernstein, 1967; Kugler and Turvey, 1987). Active forces are muscular forces produced by the subject. Passive forces are external forces, present in the environment (such as gravito-inertial forces), on which the subject obviously has no influence, but which must be taken into account to produce the desired movement. Therefore, although the subject can only produce active forces, all movements are the result of a permanent integration of active (produced) and external forces. However, although neural bases of awareness of movement outcome have been studied (Fourneret et al., 2002; Sirigu et al., 1999; Stephan et al., 2002), very little attention has been addressed to the neural mechanisms underlying awareness of produced muscle forces.

Awareness of produced muscular force is not only a theoretically interesting issue but seems to interfere constantly with movement production. Firstly, studies on tongue strength and endurance postulate that muscle force sense may be a contributing factor that limits the ability to maintain a contraction (Robin et al., 1991,

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[1] Consciousness can be defined as "inner, qualitative, subjective states and processes of sentience or awareness", and its essential feature is unified, qualitative subjectivity (Searle, 2000). In this view, motor awareness is one subjective state of awareness being part of a unified consciousness.

1992). This is also shown by the finding that during a sustained maximal contraction, TMS can evoke more force from the muscle (Taylor and Gandevia, 2001) demonstrating that a development of suboptimal output from the motor cortex underlies the decrease of muscle force. Secondly, in a patient with a stroke in the posterior limb of the internal capsule who was suffering pure motor hemi-plegia, it has been shown that motor recovery was initiated only after the effort sensation was fully recovered (Rode et al., 1996). These results show, indeed, that the sense of muscle force is not simply a *consequence* of motor behaviour but interferes with it. The awareness of force production is also an issue of importance in the discussion about the "attribution of action judgement" (Georgieff and Jeannerod, 1998; Jeannerod, 1999). Many patients with schizo-phrenia describe "passivity" experiences, in which their own actions are experienced, as though made for them by some external agent (Mellors, 1970). In most cases, the actions made by the patient, although felt to be controlled by alien forces, are not discrepant with their intentions (e.g., Spence et al., 1997). Appar-ently, these patients have a problem with the relation between intention, motor outcome and attribution of action. One might ask whether one of the causes of this problem could be related to awareness of their own produced muscular forces.

In the present study, we used functional magnetic resonance imaging (fMRI) to address the question concerning the neural bases underlying the awareness we can have of the muscle forces we put into our voluntary movement. In a reference condition, subjects performed rhythmical extension/flexion hand movements and knew in advance that in the succeeding condition, in which the resistance to the movement was higher, they would have to reproduce either their muscle forces (resulting in smaller ampli-tudes of the rhythmical movement) or the movement kinematics (resulting in higher force production to compensate for the in-creased external force). So, in this reference condition, the subjects had to gain awareness of either their produced muscle forces or of their movement kinematics. In the condition in which the muscular forces had to be reproduced, because producing the same muscular force with changed external force modifies the kinematics of the movement, the subject could not rely on movement kinematics to infer whether he or she produced the same force.

It should be noticed that, contrary to the behavioural studies cited above using the reproduction paradigm, we were interested in the neural mechanisms during the condition in which the subjects gained awareness of their muscle forces or their kinematics (refer-ence movement) and not so much in the reproduction condition. The latter condition served as a control condition for contrasting brain activation and permitted us to verify whether the subjects followed the instructions at the behavioural level. The important contrast in the present study is, therefore, that between the two reference movement conditions since this contrast might be able to elucidate cerebral processes underlying awareness of produced muscle force without varying the behavioural output.

Although, to our knowledge, no neuro-imaging study has addressed this issue in this direct way, some reports in the literature can lead us to certain predictions. Results of hypnotic manipulation studies suggest that anterior insular cortex, thalamus and anterior cingulate cortex might be important cerebral cortical structures involved in the process of consciously integrating one's effort sense (Williamson et al., 2001, 2003). So, if awareness of muscle force production is related to sense of effort (Gandevia, 1987), we can expect to find activity in these structures for the condition in which the subjects gain awareness of their force production.

As already stated above, in the present experiment (as in all reproduction paradigms), the subjects not only had to obtain some rough awareness of their produced force but had to reproduce it precisely. So, precise evaluation of the produced muscle force was necessary. This precise evaluation might be based on reafferent information. Some results show that peripheral signals of intra-muscular tension can directly reach consciousness (McCloskey et al., 1974; Roland and Ladegaard-Pedersen, 1977). In parallel, it has been shown that Golgi tendon organs, informing about intramuscular tension, project to the sensorimotor cortex (McIntyre et al., 1984). It is also known that consciousness of somatosensory stimuli needs an implication of associative sensory areas (e.g., Preißl et al., 2001). So, if awareness of produced force is mostly based on reafferent information, then substantially more activation of the primary and secondary somatosensory and associative sensory areas might be expected in the reference movement condition preceding the reproduction of force than in that preced-ing the reproduction of movement kinematics.

Methods

Subjects

Fifteen normal right-handed volunteers (12 females and three males, aged 18–37 years) participated in this study. Subjects were screened for MRI compatibility during a medical visit. All subjects gave written informed consent and were paid for their participa-tion. The experiment was approved by the local ethic committee (CCPPRB Marseille 1, ref. 01/14).

Protocol and experimental design

In this experiment, blood–oxygen level-dependent (BOLD) fMRI activity measures were used to investigate brain activity associated with awareness of produced muscular force during movement execution. Subjects made rhythmical movements with their right hand. In the "key" condition, they had to gain awareness of their active force production during the movement (Ref_Force) to reproduce this force in a succeeding condition for which they knew that the external force was going to be higher (Repro_Force). As already stated above, since the movement is the result of the interaction of active and external forces, when external force is modified, the subjects cannot rely on the movement kinematics to reproduce their active forces. Indeed, if they produce the same muscular forces, the amplitude of the movement will change. We compared these conditions with that in which they had to be aware of the kinematics (i.e., amplitude and frequency) of their movement (Ref_Mov) to reproduce it in the succeeding condition, also with a higher external force (Repro_Mov).

It must be noted that the instruction to the subjects was to accurately reproduce either muscle forces or movement kinematics in the reproduction conditions. So, for them, the "experimental" conditions were the reproduction conditions, they were not told of the importance of the reference conditions. Similarly, they were not told of the particular importance of the force conditions: both force and kinematics conditions were presented with equal importance.

To vary the external force, the subject had a manipulandum attached to the right forearm and hand over the wrist joint. This manipulandum was an fMRI-compatible mechanically jointed arm, only allowing flexion and extension movements at the wrist level. A

laterally attached lever allowed the internal friction of the manipulandum to be varied. The lever had two possible positions: high and low internal friction. During the experiment, the subjects easily changed the lever position themselves in response to an instruction given on a screen. A potentiometer was fixed on the rotation axis of the manipulandum to record the subjects' wrist movements.

The subjects were trained to perform a rhythmical preferential movement of the wrist with a self-chosen frequency that they had to maintain during the whole experiment, that is, independent of the external force level. The amplitude of the movement varied according to the experimental condition, that is, the amplitude had to be similar for the Ref_Force, Ref_Mov and Repro_Mov conditions, but should be smaller for the Repro_Force condition.

The "force" and "kinematics" conditions were alternated throughout the experiment. Because the Repro_Mov condition was rather strenuous for some subjects (same kinematics as in the Ref_Mov condition but with higher external force), we introduced a rest condition after each Repro_Mov condition in which the subjects did not move (REST). So, the order of conditions was the following: REST–Ref_Force–Repro_Force–Ref_Mov–Repro_Mov. (Note that we did not vary the order between the force and movement conditions relative to the REST condition. This was done to avoid interference between potential fatigue induced by the Repro_Mov condition and muscle force awareness.) This block of five conditions was repeated 10 times per session. With each condition lasting 32.5 s, one session took 14 min. The experiment was performed in two sessions.

During the scanning, the subjects lay on their back on the MRI bed with their right forearm in semi-supination fixed in the manipulandum and placed on their belly. To avoid any head movements, their arm and manipulandum were then comfortably fixed to their body and to the bed (but still allowing free movements of the wrist). Although they had been trained to know the order of experimental conditions, instructions were presented on a computer screen, reflected in mirror glasses fixed to the subject's head. At the start of each condition, the required internal friction level of the manipulandum was indicated to the subject (by + or −, indicating whether the resistance should be increased or decreased) together with the new movement condition. The subject changed the lever position rapidly and started moving according to the movement instruction. The instruction concerning the resistance level disappeared after 2.5 s while that for the type of condition remained during the whole block. Since subjects were well trained before passing into the machine, they usually needed less than 2.5 s to change the lever position. For the following 30 s, they performed the rhythmical movements according to the experimental condition. During the REST condition, no instruction concerning the lever position was given, and the subjects rested during 32.5 s.

It must be noticed that the subjects never (not even during the training session) received feedback about their behavioural performance because we wanted to avoid the possibility that the subjects simply "learned" the amplitude of the movements in the condition Repro_Force instead of having to gain awareness of their force production in the condition Ref_Force.

Data acquisition

Behavioural data

The rhythmical hand movements were recorded by sampling the signal from the potentiometer at a frequency of 100 Hz by a Labview program (Labview 6.1) and saving it on a hard disk for off-line analysis. For each experimental condition, the recording of the movement started 2.5 s after the beginning of the condition (when the instruction concerning the lever position disappeared on the computer screen) to give the subjects time to change the lever position of the manipulandum. As stated before, the subject had usually already started moving when recording started.

fMRI data

Imaging was performed using the 3T whole-body imager MEDSPEC 30/80 AVANCE (Bruker) of the fMRI centre in Marseille. For all participants, the experiment began with the acquisition of a high-resolution structural T1-weighted image (15 min) (voxel size $1 \times 0.75 \times 1.22$ mm). Functional imaging was then performed in two separate runs (of each 14 min) with a 3- to 5-min break between sessions. The functional images were acquired using a T2*-weighted echo-planar sequence at 30 axial slices. (Repetition time 2.5 s, interleaved acquisition, slice thickness 3 mm, inter-slice gap 1 mm, 64×64 matrix of 3×3 mm voxels). The slices covered the whole brain and were acquired parallel to the Anterior Commissure Posterior Commissure (AC-PC) plane. Every condition lasting 32.5 s, 13 volumes were acquired per condition. With every condition being repeated five times per session for two sessions, a total of 130 volumes was acquired for every experimental condition.

Analysis

Behavioural data

The potentiometer signals were analysed as follows. After verification that the behaviour of the subjects was stable throughout the duration of the experiment, we determined the mean movement amplitude and frequency as well as the standard deviation over the last 25 s (where the movement was stabilised) for all 10 occurrences for each condition. These values were averaged over all subjects to show the relative stability of the rhythmical movement.

fMRI data

Statistical parametric mapping software (spm'99) was used for image processing and analysis (http://www.fil.ion.ucl.ac.uk/spm/). The functional images were interpolated in time to correct for phase advance during volume acquisition, and realigned to the first image of each session. To do multi-subject analysis, the anatomical references and the realigned functional images of all subjects were transformed to a common standard space using the Montreal Neurological Institute template. For this normalisation, we used the functional images in which the areas affected by magnetic susceptibility have been masked (http://www.mrc-cbu.cam.ac.uk/Imaging/). The functional data were then spatially smoothed (3D Gaussian kernel: $10 \times 10 \times 10$ mm) and temporally filtered using a 120-s period high-pass filter and a Gaussian low-pass filter with a 4 mm of full width at half maximum (FWHM). A general linear fixed-effect model was applied to the time course of the functional signal at each voxel.

Each condition for each session was modelled by two reference waveforms: a box-car convolved with a canonical hemodynamic response function, and its derivative. The derivative permits a flexibility in the modelling of the onset and the offset of the hemodynamic response. We are interested in a

Table 1
Mean amplitude and frequency of the rhythmical movement averaged over 12 subjects for the four movement conditions, and the mean of intra-subject standard deviation

		Ref_Force	Repro_Force	Ref_Mov	Repro_Mov
Frequency (Hz)	Mean	0.53	0.55	0.53	0.51
	Mean standard deviation	0.05	0.05	0.04	0.05
Amplitude (°)	Mean	57.7	31.3	53.4	59.0
	Mean standard deviation	7.5	5.9	7.4	7.2

highly cognitive function, and the onset of the BOLD activity of such function might be less tightly linked to the start of the condition than what might be the case for lower level processes.

Data were analysed modelling the five experimental conditions plus the transition between conditions where the subject moved the lever to change the internal friction of the manipulandum. This transition has been implemented in the model by introducing a "task switch" at the start of each condition (except for the REST condition in which the lever position was not modified), with a duration of 2.5 s. So, the design matrix for the fixed effect analysis contained 26 sessions (two sessions per subject, 13 subjects) with six conditions (five experimental conditions plus the task switch) modelled by two regressors.

We analysed F-contrasts in which both regressors were taken into account. However, the brain structures for which we found significant activity differences were similar to those found with T-contrasts for the main regressor only. So, although the derivative

permitted us to increase the power of the model, in order to have direct information about the sign of activity differences between conditions we will present the results of T-contrasts for the main regressor only.

The following contrasts were of particular interest for the present study. Firstly, we contrasted the reference conditions with each other (i.e., Ref_Force versus Ref_Mov), the reference conditions with respect to their respective reproduction conditions (Ref_Force versus Repro_Force and Ref_Mov versus Repro_Mov) and the reproduction conditions with each other (Repro_Force versus Repro_Mov). Secondly, to identify the cerebral structures particularly implicated in conscious monitoring of force production (during condition Ref_Force) while simultaneously controlling for factors of non-interest, we performed the interaction (Ref_Force − Ref_Mov)−(Repro_Force − Repro_Mov). By analysing this interaction term, processes of non-interest are subtracted out and only the essential process of interest is kept.

Results of the analyses are reported using a significance threshold for active voxel of $P = 0.01$ (corrected) for all contrasts. The SPM99 coordinates were converted from MNI coordinate space to Talairach space (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html) and analysed with help of the Talairach Atlas (Talairach and Tournoux, 1988) and a Talairach Space Utility (http://www.ihb.spb.ru/~pet_lab/MSU/MSUMain.html). Clusters with an extent of at least 20 voxels were analysed.

Results

Two subjects had to be excluded from the analysis because of either excessive head movement during functional recording (superior to 4 mm), or not respecting the behavioural instructions during recording in the fMRI machine. Furthermore, the behavioural data of one subject was lost. However, this subject was well
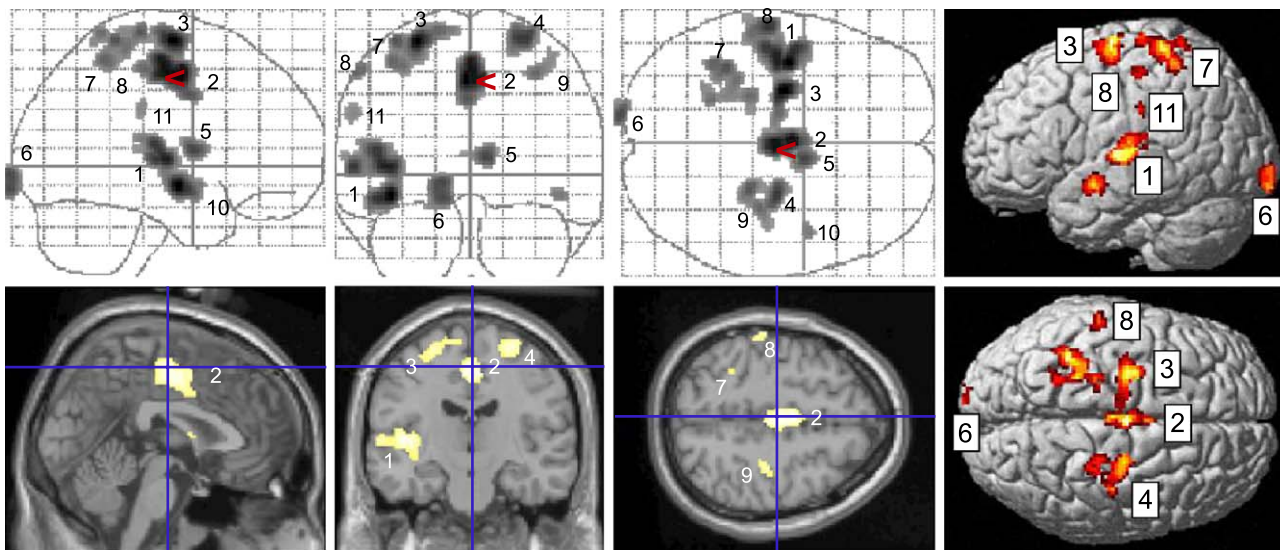

Fig. 1. Result of the t-contrast Ref_Force−Ref_Mov. Height threshold of significance: corrected $P < 0.01$ ($T = 4.90$). Voxel extent threshold: 20 voxels. The voxels, all seen in the glass brain representation, are superimposed on the spm single subject canonical brain on the anatomical slices passing through cluster 2 (Talairach coordinates [−2 −13 47]), and on the canonical brain surface rendering of spm. Cluster numbers correspond to those in Table 2. For the sake of clearness, not every cluster is numbered in each of the three glass brain views.

trained and we had already verified her behavioural data for all the experimental conditions, even inside the fMRI machine. Therefore, we decided to include this subject in the analysis of the functional fMRI data. Thus, the analysis of the behavioural data is based on 12 subjects and that of the fMRI data on 13 subjects.

Behavioural data

First of all, it should be mentioned that all subjects reported the difficulty of the force conditions. Apparently, gaining conscious-ness of produced force is difficult. The experimental conditions Ref_Mov and Repro_Mov were experienced as "easy", "natural" and not mentally demanding tasks. Although some physically less trained subjects reported that they were tired at the end of the Repro_Mov condition because of the higher resistance to the movement (which was basically the reason for introducing the REST conditions), they experienced no problem in reproducing the amplitude of the movement despite the modified external force.

The behavioural data were analysed to verify whether the subjects had indeed followed the instructions given before and during the experiment. Table 1 shows the movement amplitude and frequency for the four movement conditions averaged over the 12 analysed subjects. First of all, although between subjects the movement frequency varied from 0.3 to 0.7 Hz (with a mean of 0.5 Hz), the subjects maintained their frequency over the different conditions. Secondly, the subjects produced similar amplitudes in the conditions Ref_Force, Ref_Mov and Repro_Mov. We only found differences of about 8%: all subjects produced a slightly smaller amplitude in condition Ref_Mov relative to Ref_Force (post hoc Newman Keuls; $P < 0.001$) and relative to Repro_Mov condition ($P < 0.001$). And, finally, as expected, the movement amplitude in the condition Repro_Force decreased considerably (by about 45%).

fMRI data

Contrasts between the two reference conditions

The contrast Ref_Mov−Ref_Force did not show any significant difference in BOLD signal, indicating that no structure was more activated in Ref_Mov than in Ref_Force. However, the inverse contrast Ref_Force−Ref_Mov showed that the reference condition preceding the reproduction of force (i.e., the condition in which the subjects gained awareness of their muscular forces) implies a great deal more activation. The clusters are shown in Fig. 1 and the corresponding anatomical structures are indicated in Table 2. The most important activity difference, both with respect to the number of voxels as to the T value, was in the left posterior insula and superior temporal gyrus (BA 38 and 21) with extensions into inferior parietal lobule (cluster 1). Some activity difference was also found in the homologous structures on the right side (cluster 10). Important activity differences were found in frontal structures such as the left anterior cingulate gyrus (BA 24, 31) and the posterior part of the left medial frontal gyrus (BA 6) with extensions into homologous structures in the right hemisphere (cluster 2). More lateralised activation difference for left BA 6 was also found in cluster 3, and for right BA 6 in cluster 4, extending into primary motor cortex (M1) and primary sensory areas. Right M1 cortex was also found to be activated for cluster 9 with an activity extending into the postcentral BA 3. We found

Table 2
Results of the t-contrast Ref_Force-Ref_Mov, ordered relative to the height of T values

Cluster	Number of voxels	Coordinates of local maxima	T value	Anatomical structures
1	827	−37 −8 −8	6.27	L medial insula
		−40 −13 4	6.07	L posterior insula
		−57 −19 5	5.90	L superior temporal gyrus Extension into inferior parietal lobule
2	619	−2 −4 44	6.25	L anterior cingulate gyrus (BA 24)
		−2 −13 47	6.14	L posterior part of medial frontal gyrus (BA 6)
		−2 0 34	5.62	L anterior cingulate gyrus (BA 24) Extension into BA 31
3	298	−26 −7 61	6.23	L medial frontal gyrus (BA 6)
		−16 −10 67	5.46	L superior frontal gyrus (BA 6)
4	253	28 −12 63	5.87	R precentral gyrus (BA 6)
		24 −26 66	5.62	R central sulcus (4, 3)
5	124	8 0 7	5.77	R ventral anterior thalamic nucleus Extension into caudate body and head
6	142	−14 −99 −5	5.72	L inferior occipital gyrus (BA 17, 18)
7	426	−38 −38 63	5.64	L superior parietal lobule (BA 5, 7)
		−40 −44 54	5.48	L supramarginal gyrus (BA 40)
		−24 −26 66	5.42	L postcentral gyrus (BA 2, 3) Extension into M1 (BA 4)
8	36	−57 −23 47	5.48	L postcentral gyrus (BA 2)
9	72	34 −21 47	5.46	R postcentral gyrus (BA 3)
		42 −17 54	5.05	R precentral gyrus (BA 4)
10	25	45 4 −9	5.26	R superior temporal gyrus (BA 38) Extension into insula
11	20	−57 −28 29	5.09	L inferior parietal lobule Extension into the supramarginal gyrus (BA 40)

Cluster numbers are indicated in Fig. 1. Height threshold of significance: corrected $P < 0.01$ ($T = 4.90$). Voxel extent threshold: 20 voxels (voxel size: [2.0 2.0 2.0]). The local maxima are given in Talairach's reference space and have a minimum distance of 8 mm apart. In the column Anatomical structures, indicated are those underlying the local maxima as well as those underlying the most important extensions of the cluster. L = left hemisphere; R = right hemisphere; BA = Brodmann's area.

important activity differences for several left parietal structures, such as primary sensory areas (BA 2, 3) (clusters 7, 8) and associative sensory areas in the superior parietal lobule (BA 5, 7) (cluster 7) and for the supramarginal gyrus (BA 40) in the inferior

parietal lobule (cluster 11). Surprisingly, we also found a difference in activity in BA 17 and 18 of the left inferior occipital gyrus (cluster 6). And, finally, more activity for Ref_Force than for Ref_Mov was found for the right thalamus (cluster 5).

Reference versus reproduction conditions

The results of the t-contrast Repro_Force–Ref_Force did not show any activation above threshold, indicating that no structure was more activated in the condition in which the active force was reproduced relative to the condition in which this force was monitored or quantified.

The inverse contrast, however, showed several clusters of activation, shown in Fig. 2 and indicated in Table 3. A rather large cluster (cluster 1) was in the left postcentral gyrus and superior parietal gyrus, corresponding to activation of the left primary and associative sensory areas. This activation extended forward into M1 and backwards into the supramarginal gyrus. A second much smaller cluster of activation was found in right anterior cingulate gyrus, extending into dorsal anterior cingulate area and into medial frontal gyrus. A third cluster of activation was in the right cerebellar tonsil.

The contrasts between Ref_Mov and Repro_Mov did not show any difference in brain activity between these two experimental conditions. This means that the preparing to reproduce the kinematics against a higher external force implicates the same brain structures, with a similar activity level, as actual reproduction of the movement, despite the difference in actual force production.

Contrasts between the two reproduction conditions

The preceding contrasts showed enormous differences in brain activity between the condition in which the subjects had to gain awareness of their force production to reproduce it later on and that during which they had to gain awareness of the kinematics of their movement to reproduce it. However, the contrasts between the two

Table 3
Results of the t-contrast Ref_Force–Repro_Force, ordered relative to the height of T values

Cluster	Number of voxels	Coordinates of local maxima	T value	Anatomical structures
1	821	−32 −32 59	6.85	L postcentral gyrus (BA 3)
		−22 −43 65	5.83	L postcentral gyrus (BA 2)
		−24 −48 49	5.17	L superior parietal gyrus (BA 5, 7)
				Extension into M1 (BA 4) and the supramarginal gyrus (BA 40)
2	27	18 32 19	5.59	R anterior cingulate gyrus Extension into BA 32 and into the medial frontal gyrus (BA 9)
3	24	44 −48 −35	5.50	R cerebellar tonsil

Cluster numbers are indicated in Fig. 2. Height threshold of significance: corrected $P < 0.01$ ($T = 4.90$). Voxel extent threshold: 10 voxels (voxel size: [2.0 2.0 2.0]). The local maxima are given in Talairach's reference space and have a minimum distance of 8 mm apart. In the column Anatomical structures, indicated are those underlying the local maxima as well as those underlying the most important extensions of the cluster. L = left hemisphere; R = right hemisphere; BA = Brodmann's area.

corresponding reproduction conditions did not show similar differences in activity. We did not find any structures more activated in Repro_Mov than in Repro_Force, and only one structure more activated in Repro_Force than in Repro_Mov, namely BA 17, 18 in the left inferior occipital gyrus. We had already found this structure activated for the contrast Ref_Force–Ref_Mov (Cluster 6 in Table 2). It appears that the experimental conditions related to muscle force awareness and reproduction evoke (more) activation in this visual structure than the conditions related to monitoring and reproducing kinematics.
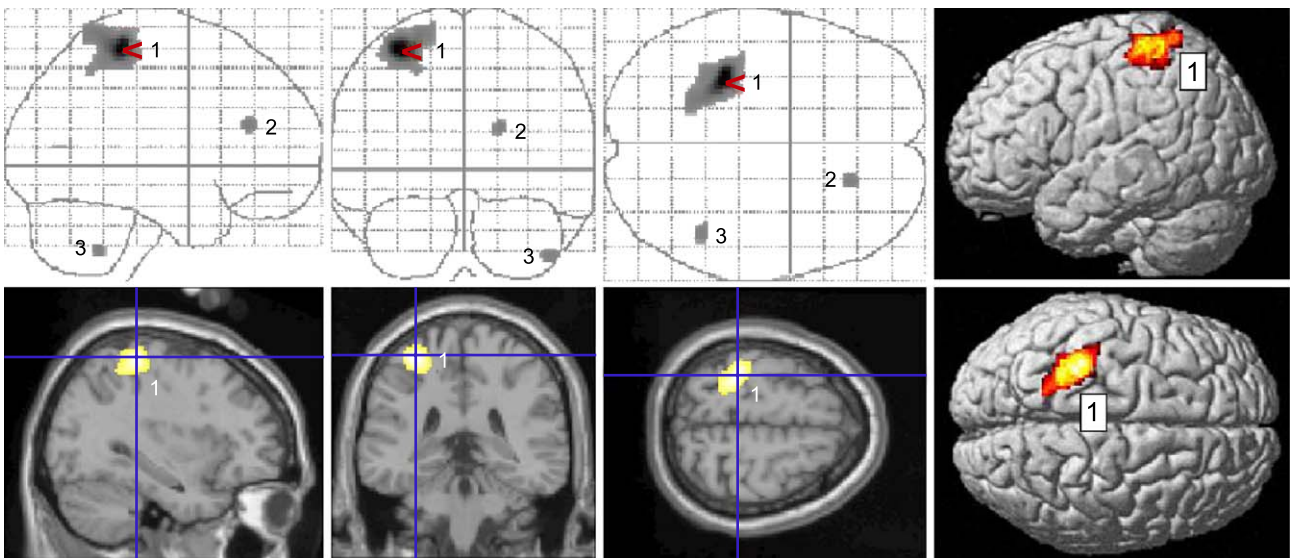

Fig. 2. Result of the t-contrast Ref_Force–Repro_Force. Height threshold of significance: corrected $P < 0.01$ ($T = 4.90$). Voxel extent threshold: 20 voxels. The voxels, all seen in the glass brain representation, are superimposed on the spm single subject canonical brain on the anatomical slices passing through cluster 1 (Talairach's coordinates [−32 −32 59]), and on the canonical brain surface rendering of spm. The numbers indicating clusters correspond to those in Table 3.
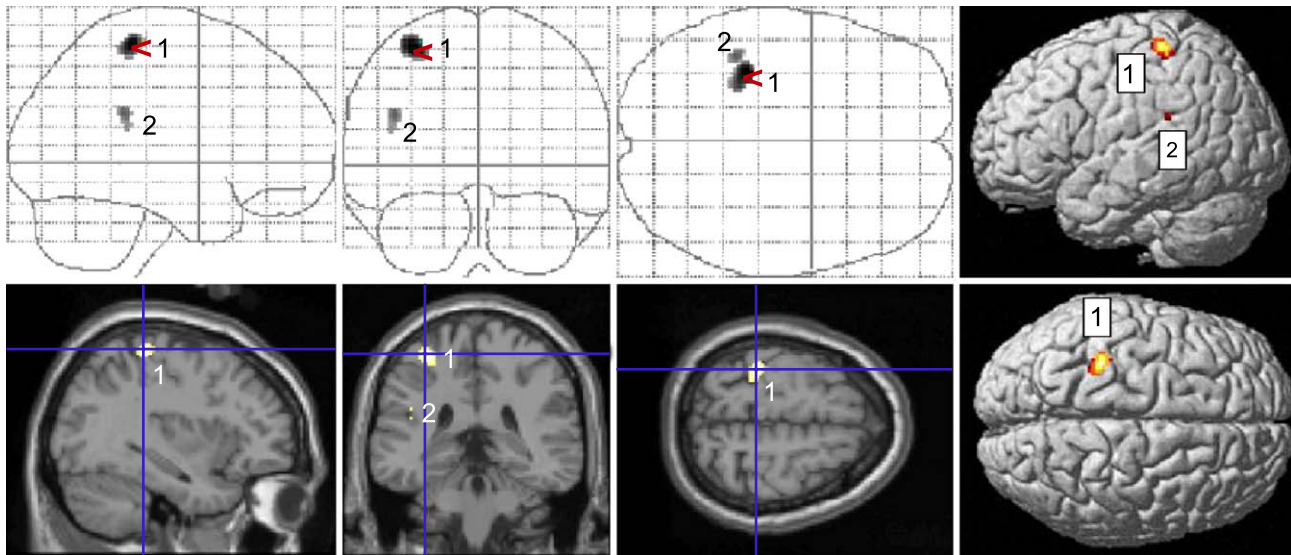
Fig. 3. Result of the contrast (Ref_Force − Ref_Mov)–(Repro_Force − Repro_Mov), showing the structures specifically implicated in conscious force extraction. Height threshold of significance of masking: corrected *P* < 0.01 (*T* = 4.90). Voxel extent threshold: 20 voxels. The voxels, all seen in the glass brain representation, are superimposed on the spm single subject canonical brain on the anatomical slices passing through Talairach coordinates [−26 −36 55], and on the canonical brain surface rendering of spm. Cluster numbers correspond to those of Table 4.

Interaction between the four movement conditions

The difference between conditions for the contrasts shown so far do not give unambiguous information about which structures are implicated in awareness about muscle force in movement production since this process is not the only functional difference between the conditions. With the contrast (Ref_Force − Ref_Mov)–(Repro_Force − Repro_Mov), we isolate the process of gaining awareness of produced muscle force from other processes of non-interest, such as, for instance, the process of memorisation of information for later reproduction, or processes related to the need to ignore the kinematics in the Repro_Force condition (something the subjects reported repetitively), both of which influence the contrast Ref_Force–Repro_Force. Furthermore, differences in "difficulty" between being aware of muscle force and being aware of kinematics (also reported repetitively by the subjects) might influence the contrast Ref_Force–Ref_Mov.

So, to extract the cerebral activity specifically implied in gaining awareness of muscle force, while controlling for the processes of non-interest, a *t* test was performed on the contrast (Ref_Force − Ref_Mov)–(Repro_Force − Repro_Mov). Other functional differences between Ref_Force and Ref_Mov than the one that we are interested in can be expected to be similar for the conditions Repro_Force and Repro_Mov.

The result of this analysis is given in Fig. 3 and Table 4. Two clusters were found. The anatomical structures underlying cluster 1 are left BA 3 with extensions into M1 (BA 4) and BA 2. The second cluster was in the left inferior parietal lobule with an extension into the posterior part of the insula. So, it appears that gaining awareness of muscle force production and quantifying it, mostly implies activation of primary sensorimotor area.

Discussion

This study was performed to gain insight into the cerebral processes involved in awareness of our active muscle forces during movement production, or, in other words, in awareness of the means we have to precisely realise our desired movements. An important contrast to consider is therefore that between the two reference movement conditions (Ref_Force and Ref_Mov). In these conditions, the behavioural output was similar, that is, the subjects performed a rhythmical movement with similar amplitude and frequency. However, the fact that, later on, they had to reproduce either the force or the kinematics against a higher resistance put them, as we expected, in a different cognitive context. Obviously, their awareness had not the same content. It appeared that the contrast between Ref_Force and Ref_Mov was highly asymmetrical. We did not find any brain structure more activated in the Ref_Mov condition than in the Ref_Force condition, whereas several structures were much more activated in the Ref_Force condition than in the Ref_Mov condition. In fact, for none of the other experimental conditions was more activity found

Table 4
Results of the t-contrast (Repro_Force − Repro_Mov)–(Ref_Force − Ref_Mov), ordered relative to the height of *T* values

Cluster	Number of voxels	Coordinates of local maxima	*T* value	Anatomical structures
1	106	−34 −32 59	5.85	L postcentral gyrus (BA 3) Extensions into M1 (BA 4), BA 2
2	27	−42 −38 26	5.25	L inferior parietal lobule Extension into posterior insula

Cluster numbers are indicated in Fig. 3. Height threshold of significance: corrected *P* < 0.01 (*T* = 4.90). Voxel extent threshold: 20 voxels (voxel size: [2.0 2.0 2.0]). The local maxima are given in Talairach's reference space. In the column Anatomical structures, indicated are those underlying the local maxima as well as those underlying the most important extensions of the cluster. L = left hemisphere; R = right hemisphere; BA = Brodmann's area.

in any cerebral structure than in the Ref_Force condition. Secondly, no significant difference in cerebral activity was found between the conditions Ref_Mov and Repro_Mov. We will first discuss this latter result and then discuss the first, and most important, result.

Awareness of the kinematics of the movement

The experimental conditions Ref_Mov and Repro_Mov, although different from the point of view of the muscular forces produced, showed in fact similar cerebral activity. One could have expected more activity in the motor areas in the Repro_Mov condition in which the subjects produced larger forces, since it has been shown that the level of the fMRI signal is correlated with the amplitude of the muscular force output (e.g., Dai et al., 2001). However, the correlation between force output and BOLD level has mainly been shown in static situations for which the goal of the action was simply to produce a force, whereas our subjects produced dynamic muscular forces to move their hand. Moreover, in these studies, often large ranges of force were studied (sometimes going to 80% of maximal force, as in Dai et al., 2001), whereas in the present study, the external forces in the Ref_Mov and Repro_Mov conditions could not be that different for experimental reasons (the subjects had to be able to move their hand in the Repro_Force condition while applying the same forces as in the Ref_Force condition). Finally, it has been shown that the production of small forces can, in certain conditions of high attention and precision demands, activate motor areas at a higher level than large forces (Ehrsson et al., 2000; Kuhtz-Buschbeck et al., 2001). So, the relation between force output and activity of the cortical motor areas is not simple and is influenced by other factors.

Awareness of kinematics seems to be easily accessible and movement kinematics is easily reproducible independent of external forces. Indeed, many behavioural studies have shown our capability to produce the same kinematics in various environmental conditions. For example, studies in microgravity showed that in the face of a continuous drop from hypergravity to microgravity, the subjects were capable of intentionally maintaining the same spatiotemporal movement properties throughout the variation in gravity (Bonnard et al., 1997). Viviani and Terzuolo (1983) showed the facility that we have in producing the same kinematics with different effectors although the produced forces are very different. It appears that the integration of the external forces with our self-produced muscular forces to produce a given movement kinematics is natural. The present study shows the reflection of this at the cerebral level.

Brain areas involved in awareness of produced muscle force

Insula

The most significant activity difference between Ref_Force and Ref_Mov was found for the posterior part of left insula (and not for the anterior part of the insula, as hypothesized in the introduction). A collective consideration of afferents and efferents shows that the insula has connections with principal sensory areas, with association areas, with paramotor cortex (e.g., BA 6) and cingulate areas (Mesulam and Mufson, 1982; see also Ture et al., 1999). The topographic distribution of efferent cortical output of the posterodorsal insula suggests it to be specialised for auditory–somesthetic–skeletomotor functions (Mesulam and Mufson, 1982). Indeed, intracortical stimulation of posterior insular cortex evokes somesthetic sensation (Ostrowsky et al., 2000). Moreover, patients with acute stroke restricted to the posterior insula can show somatosensory deficits (Cereda et al., 2002). Also, somatosensory tactile tasks activate the posterior insula (Sadato et al., 2000). These results strongly suggest that the posterior insula is part of a somesthetic network. The finding in the present study of the important activation of the posterior insula in the condition Ref_Force seems to indicate the importance of somesthetic information processing in awareness of produced muscle force.

Somatosensory areas

This is also shown by the important activity in primary and associative sensory areas in the condition Ref_Force relative to all other conditions (cluster 7 in Fig. 1 and Table 2; cluster 1 in Fig. 2 and Table 3; cluster 1 in Fig. 3 and Table 4). Although in the conditions Ref_Force and Ref_Mov, the subjects received similar somatosensory information concerning their actual movements (because the movements were similar), it appears that this information had ''more importance'' in the condition Ref_Force.

Lesion (Caselli, 1993; Levine et al., 1978) and stimulation studies (Penfield and Jaspers, 1954) have suggested that areas posterior to SI (BA 5, 7 and 40) are necessary for the conscious processing of somatosensory stimuli. Studies in neurosurgical patients showed that subliminal stimuli (i.e., not reaching consciousness) elicit only the early component of the evoked potentials in the primary somatosensory cortex (Libet et al., 1967). Recently, it was shown in a MEG study on tumour patients that activation of the primary somatosensory cortex alone is not sufficient to have consciousness about tactile events (Preißl et al., 2001). These patients showed an intact early (40 ms) component and an absence of later components as well as a complete lack of conscious awareness of tactile stimuli. These results together strongly suggest that activation of associative sensory areas is necessary to obtain consciousness about an (external) event.

The need to reproduce the force required, as already stated in Introduction, an awareness with a precise content. Since the subjects had to reproduce the muscle force independently of the kinematics of the movement (the kinematics were to change in the Repro_Force condition), the subjects had to separate the relevant from the irrelevant afferent information. Muscle spindle activity, besides the fact that it is highly influenced by kinematics, does not seem to be a good candidate for muscle force estimation (McCloskey et al., 1974). Although Golgi tendon organs give reliable information concerning intramuscular tensions, it is evident that their discharge is also influenced by the kinematics of the rhythmical movements (that, the subjects knew, was going to change). So, the subjects could not use these proprioceptive sources to calibrate their produced force. The only afferent information that the subject could use seems to be the cutaneous information coming from the hand pushing the handle of the manipulandum. It has been shown in experiments with skin surface anaesthetics that cutaneous information may play a role in grip force regulation (e.g., Monzee et al., 2003) and weight estimation (Gandevia and McCloskey, 1977). It is interesting to note that a small but significant activation difference in right cerebellar tonsil was found for the simple main effect of Ref_Force−Repro_Force (cluster 3 in Fig. 2 and Table 3). The lateral cerebellum is likely to have a role in sensory discrimination (Liu et al., 2000; Parson et al., 1997).

Anterior cingulate cortex

Another very important activation difference between Ref_Force and Ref_Mov was found for anterior cingulate cortex (ACC). No difference in this structure was found for Ref_Force relative to Repro_Force (only a small cluster of activation anterior in right ACC). A large metaanalysis of PET studies (Paus et al., 1998) showed that the common denominator of ACC activation across many task conditions is in fact the amount of effort which has to be engaged in a task. ACC activation, therefore, might reflect the degree of intentional effort, motivation or volition that is needed to carry out a task (Paus, 2001; Winterer et al., 2002). So, the important activation difference in this region in the present study probably reflects the inhabitual aspect of the "force" conditions: gaining awareness of the produced force underlying a movement costs an important amount of volition.

Left inferior parietal lobule

We found this structure for both the simple main effect Ref_Force – Ref_Mov and the interaction (Ref_Force − Ref_Mov)–(Repro_Force − Repro_Mov), that is, the contrast showing the pure "gaining precise awareness" of produced muscular forces. The role of left inferior parietal lobule in motor attention has been clearly demonstrated (e.g., Rushworth et al., 2001a,b). In parallel, the inferior parietal lobule is generally assumed to be involved in "sensory awareness". This assumption is based on the fact that neglect, which constitutes an attentional rather than a sensory deficit, is most commonly found after lesions of the inferior parietal lobule (Mattingley et al., 1998).

General considerations about awareness of produced force

It is clear that gaining precise awareness of the produced force underlying a movement is a demanding task. At a behavioural level, all subjects reported the difficulty of the force tasks relative to the kinematics tasks. This, together with the very important cerebral activity in the Ref_Force condition relative to the other conditions, show that gaining awareness in such a precise way that one is able to reproduce the muscular forces we put in a movement despite changing external force, is not easily accomplished.

There might be two reasons for this difficulty. Firstly, it has been proposed that the level of processing which relates to the "public" aspects of an action may be conscious, whereas the "private" aspects are not shareable with other individuals and, therefore, remain unconscious (Frith, 1995). Indeed, awareness of forces seems to be merely related to the external (i.e., public) force ("There is wind opposing to my movement", something that can be shared with others) and not to the produced (private) force ("I had to produce more force to maintain my walking speed"). Reports concerning awareness of force production published so far are often related to weight estimation (e.g., Burgess and Jones, 1997; Gandevia and McCloskey, 1977; Rode et al., 1996). Weight estimation is always with respect to an object, so the awareness concerns more the object (i.e., the public aspect) than the muscular force produced by the subject (although, of course, the produced force has to be taken in account at some, unconscious, level to be able to perform the task). So, one difficulty of the Ref_Force condition might have been to obtain awareness of some private aspect that usually does not reach consciousness.

Secondly, as already argued above, reproduction requires a precise and not some rough awareness. Besides the fact that during a desired action, produced muscle forces change all the time, we have to separate the relevant from the irrelevant afferent information. Indeed, usually, sensory signals inform us about movement dynamics "as a whole", taking also into account movement kinematics. So, it seems to be difficult to obtain precise awareness of something that changes all the time, and for which we have to discriminate the different sources of sensory information.

In a review paper, McCloskey (1978) argued that the judgements of achieved muscular force are based on the magnitudes of the outgoing motor commands rather than on the real muscular tensions achieved. This hypothesis seems not to be confirmed by the present results. Indeed, all brain areas we found activated in the present experiment taken together suggest that awareness of produced force is essentially based on activation of primary and associative somatosensory structures, that is, on sensory information. Moreover, a parallel is often made between muscle force sense and effort sense (Gandevia, 1987). However, it is known that the anterior insular cortex is an important cerebral cortical structure involved in the process of integrating one's sense of effort (Williamson et al., 2001, 2003), and in our study, we did not find any activity difference in this structure between the Ref_Force condition and the other conditions. So, although often used interchangeably, awareness of muscular force does not seem to be based on the same mechanism as that underlying the integration of one's sense of effort.

Conclusion

The present study showed, firstly, that, contrary to awareness of the kinematics of our movements, awareness of the muscular forces in movement production is not easily accessible. In other words, although we easily can have awareness of the movement we are realizing (i.e., of the integration of "private" and "public" forces), the same does not hold for awareness of the private forces underlying that realisation. Secondly, the fMRI results strongly suggest that muscular force awareness is merely based on sensory information processing and not so much on the magnitude of outgoing motor commands. Finally, our results suggest that the neural bases seem to be clearly distinct, and so awareness of muscular forces should not be confounded with sense of effort.

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