BRAIN RESEARCH 1620 (2015) 98–106

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Research Report

Activity in the brain network for dynamic manipulation of unstable objects is robust to acute tactile nerve block: An fMRI study

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ARTICLE INFO

Article history:
Accepted 11 May 2015
Available online 19 May 2015

Keywords:
Manipulation task
Spring compression test
Motor task
Dorsal premotor cortex
Local anesthesia
fMRI

ABSTRACT

Objective: To study whether a temporary block of the tactile afferents from the fingers causes altered activity in the neural network for dexterous manipulation. *Methods:* Whole-brain functional Magnetic Resonance Imaging (fMRI) was conducted in 18 healthy subjects, while they compressed an unstable spring between the thumb and index finger of the right hand. Two sensory conditions – with and without tactile input from the fingers – were employed. In the latter condition the digital nerves were blocked by local anesthesia. *Results:* Compression of the unstable spring was associated with activity in an earlier described network for object manipulation. We found that this entire network remained active after a nerve block, and the activity was increased in the dorsal premotor cortex. *Conclusions:* The neural network for dexterous manipulation is robust with only minor alterations after acute loss of tactile information from the fingers. There was no loss of activity, but, unexpectedly, an increased activity in some parts of the network. *Significance:* This study gives new insights to possible neural compensatory mechanisms that make fine motor control possible after acute disruption of tactile information in natural situations like cold weather or wearing surgical gloves.

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http://dx.doi.org/10.1016/j.brainres.2015.05.016
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1. Introduction

Performance of dexterous tasks requires precise dynamical control of amplitude and direction of fingertip force vectors and depends profoundly on visual, tactile and proprioceptive inputs (Flanagan et al., 2006; Valero-Cuevas et al., 2003). Tactile information from the digits is thought to be essential for the on-line monitoring of object manipulation, and various types of tactile receptors provide information about different stages of the manipulative task, including information on timing, magnitude and direction of the fingertip forces that is used to adapt the fingertip forces to the physical properties of the object (Johansson and Flanagan, 2009). It has been shown that fast adapting cutaneous receptors in the fingertips can detect small tensions in the skin and microslips between the hand and the object surface. Despite the importance of tactile input for object manipulation, however, it is routinely possible to grasp and manipulate objects well after disruption of tactile input in natural situations like in cold weather or when wearing surgical gloves – or even in experimental settings after blocking the tactile input by cutaneous anesthesia – although, if the object is stable, with at an elevated grip force level in order to have a safety margin (Westling and Johansson, 1984; Johansson and Cole, 1994; Nowak et al., 2001). However, when trying to handle an unstable object with anesthetized fingers, e.g. a buckling spring, less force than normal is used because of concern not to tip over the edge of instability (Venkadesan et al., 2007).

Earlier functional neuroimaging studies identified a bilateral fronto-parietal-striatal network for object manipulation (dorsal and ventral premotor cortex, SMA, CMA, insula, intraparietal cortex and basal ganglia) that is active during dexterous manipulation (Binkofski et al., 1999a, 1999b; Ehrsson et al., 2000, 2001; Kawashima et al., 1998; Kuhtz-Buschbeck et al., 2001, 2008). In recent fMRI studies manipulation of unstable objects, which puts a larger demand on the on-line control of the fingertip forces preventing the object to buckle and slip out of the hand, was investigated (Mosier et al., 2011; Holmstrom et al., 2011). The unstable objects were constructed by compression springs that can be built with different requirements for strength (i.e., stiffness) and dexterity (i.e., propensity to buckle), respectively (Valero-Cuevas et al., 2003, Dayanidhi et al., 2013). It was discovered that specific parts of the network for dexterous manipulation are more involved in the control of the direction of the fingertip force vector (i.e., bilateral primary motor cortex, left premotor cortices and intraparietal sulcus, right somatosensory cortex and bilateral cerebellum), while different parts of the left primary sensory–motor cortices and bilateral cerebellum are more involved in the control of force magnitude.

In this study we investigated how the activity in the neural network for dynamic manipulation of unstable objects was influenced when the tactile information from the fingertips was blocked, thus removing a crucial source for on-line control of fingertip forces. In particular, we wanted to see whether there was a difference in the part of the network that

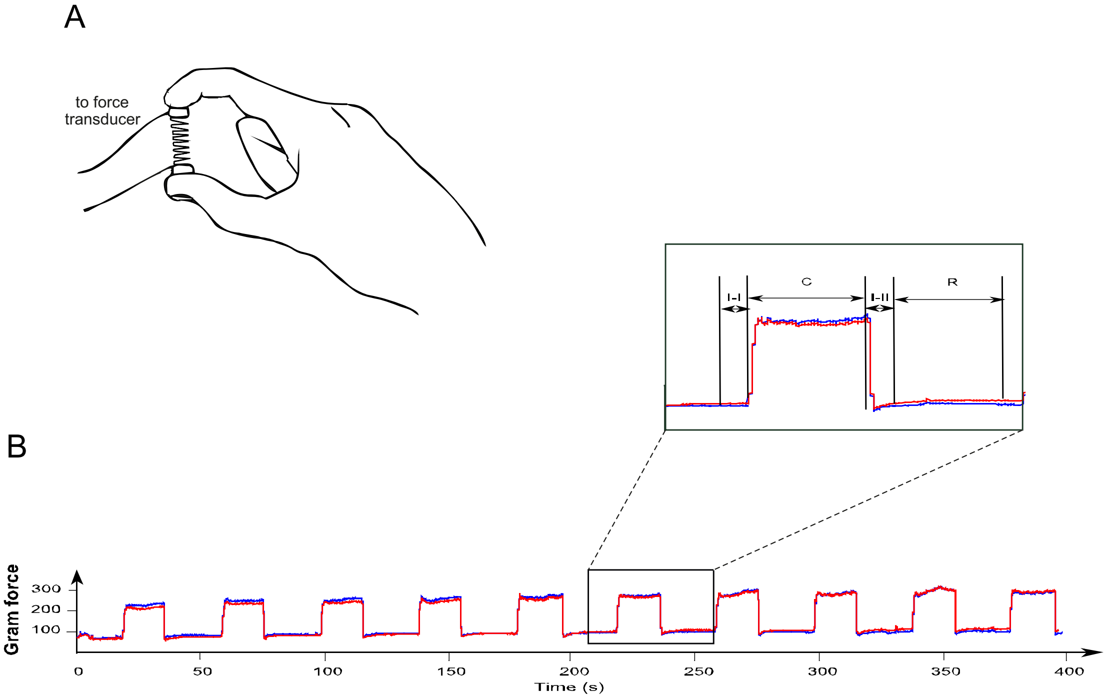

Fig. 1 – A. The spring compression task. The spring held between the thumb and index finger is supposed to be compressed as much as possible without buckling. The level of compression is indicative of the neural control capabilities to stabilize dynamic manipulation. B. Force recording during performance of the spring compression task. Blue line – thumb, red line – index finger. 10 cycles of spring compressions were performed for each sensory condition. Inset I-I – 5 s of verbal instruction I, C – 15 s of sustained spring compression, I-II – 5 s of verbal instructions II and R – 15 s of rest.

was more engaged in fingertip force vector direction control than in force magnitude control.

2. Results

2.1. *Task performance*

The participants could perform the sustained spring compression task with cutaneous anesthesia of the thumb and index finger. However, the mean fingertip force with ordinary sensation was significantly higher (198.8 g±40.2 (mean±SD)), than with anesthesia (166.7 g±44.4; $p=0.019$) (Fig. 2A). Yet, the stability of the fingertip forces (SD, see Section 4) during the plateau periods was similar in the two conditions (Fig. 2B). In the pilot subgroup of six subjects task performance without tactile and visual input was not possible.

2.2. *Brain activation with and without tactile input.*

2.2.1. *Conjunction between contrasts Compression(T)–Rest(T) and Compression(noT)–Rest(noT)*

Conjunction analysis was performed to reveal activations during the task performance common for both conditions, i.e., contrasts: Compression(T)–Rest(T) and Compression (noT)–Rest(noT). A widespread bilateral network of areas was found (Fig. 3, Table 1). The largest cluster of activation included the left sensory–motor cortex and supramarginal gyrus. Large clusters were also observed bilaterally in insula. Both of these later clusters extended to pallidum, and right – to precentral gyrus (PMv). On the right side of the brain, the largest cluster of activation was in the intraparietal sulcus.

2.2.2. *Comparison between two conditions*

Anasthesia did not cause any decrease in activity in any part of the brain: comparisons of images during spring compressions in the contrast Compression(T)–Compression(noT), showed no significant difference.

On the other hand, contrast Compression(noT)–Compression(T) showed one cluster of significant activation bilaterally in the dorsal premotor cortex (Fig. 4, Table 1).

3. Discussion

The aim of the present study was to compare the neural network for dynamic manipulation during a dexterous task before and after acute removal of tactile input by a digital nerve block. We found that brain activity with full access to tactile information did not exceed cortical activity without tactile information in any part of the brain: all activity present with tactile input was also present without tactile input. This corresponded to a successful task performance in both conditions as the subjects were able to compress the spring, albeit to a different level of instability.

In previous studies, anesthesia to the fingers has led to higher finger forces during manipulation of the stable objects, presumably to obtain larger safety margins (Westling and

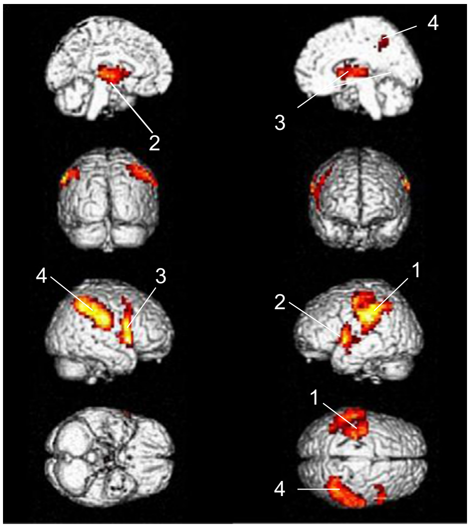

Fig. 3 – Significant activations from the conjunction analysis between contrasts Compression (T)–Rest (T) and Compression (noT)–Rest (noT) (cluster-level correction, FWE, $p<0.05$, number of voxels$>$400) on three-dimensional rendering of the anatomical template (SPM-96). The significant clusters of activations are presented in Table 1.

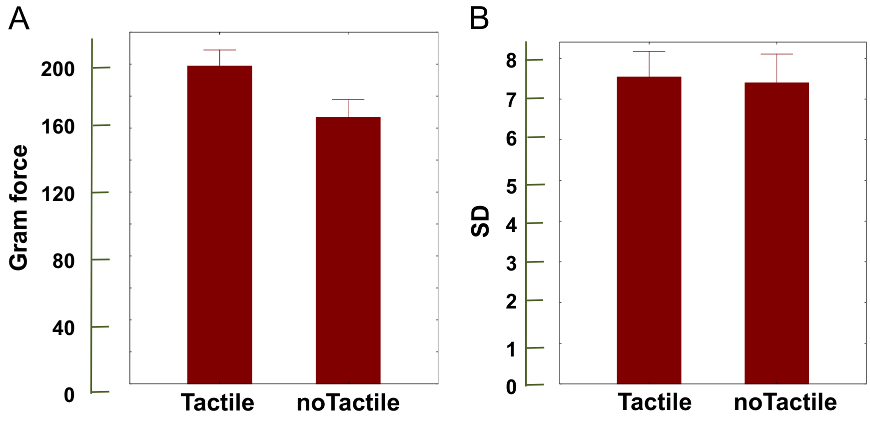

Fig. 2 – A. Mean force (+SE) produced during the performance of the spring compression task with and without tactile modality. B. Variation of the grip force (mean SD (+SE)). The recording of the force was done outside of the MR camera in the separate experiment.

Table 1 – Contrasts[*]

Area	Cluster-level	Peak-level		x	y	z
	P_{FWE}	T	Z			
Conjunction between Compression(T)–Rest(T) and Compression(noT)–Rest(noT) conditions						
1. Left postcentral gyrus (S1)	**0.001**	**5.45**	**4.55**	**−31**	**−24**	**36**
Left supramarginal gyrus		4.14	3.71	−48	−28	23
Left supramarginal gyrus		4.18	3.71	−55	−31	36
2. Left insula	**0.008**	**5.15**	**4.36**	**−41**	**0**	**5**
Left superior temporal gyrus		3.77	3.40	−41	−14	0
Left pallidum		3.59	3.27	−17	0	5
3. Right insula	**0.005**	**4.22**	**3.73**	**45**	**7**	**0**
Right superior frontal gyrus (PMv)		4.15	3.68	55	7	23
Right pallidum		3.73	3.38	21	0	5
4. Right supramarginal gyrus	**0.001**	**4.21**	**3.73**	**58**	**−21**	**27**
Right intraparietal sulcus		4.15	3.68	41	−45	41
Right supramarginal gyrus		3.98	3.56	48	−24	36
Contrast Compression(noT)–Compression(T)						
Right precentral gyrus (PMd)	**0.017**	**4.90**	**4.20**	**17**	**−14**	**63**
Left precentral gyrus (PMd)		3.70	3.35	−21	−17	50

[*] Cluster-level correction (FWE, $p<0.05$), >400 voxels.

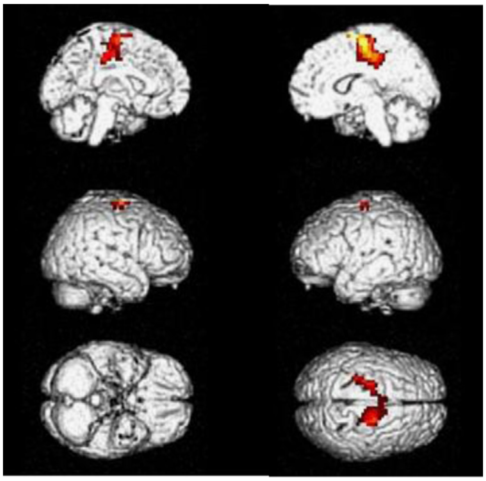

Fig. 4 – Significant activations in the contrast Compression (noT)–Compression (T) (cluster-level correction, FWE, $p<0.05$, number of voxels >400) on three-dimensional rendering of the anatomical template (SPM-96). The significant clusters of activations are presented in Table 1.

Johansson, 1984; Johansson and Cole, 1994; Nowak et al., 2001). An opposite effect is observed for the unstable spring compression task in the present study: the task is performed with lower force under local anesthesia. Contrary to the simpler tasks with stable objects, the spring compression task is constructed to determine maximal sensorimotor performance capabilities (Dayanidhi et al., 2013) and is therefore sensitive to deficit in sensorimotor integration, as reported in a similar sensory occlusion study (Venkadesan et al., 2007). Since the maximal sensorimotor performance capability is expressed by the maximal level of compression of the spring, lower force is expected when sensorimotor integration is somewhat compromised as in case of tactile input block.

The network, activated in both sensory conditions in the present study, corresponds to a well described network for object manipulation including sensory–motor and premotor areas, intraparietal cortex, insula, cerebellum and basal ganglia (Binkofski et al., 1999a; Ehrsson et al., 2000, 2001; Kawashima et al., 1998; Kuhtz-Buschbeck et al., 2001, 2008; Holmstrom et al., 2011; Mosier et al., 2011). So, similar brain mechanisms, both with and without tactile information, appear to support on-line task monitoring and operation of the internal models involved in performance of dexterous tasks.

3.1. *Role of other sensory modalities*

Participation of the dexterity network in the on-line monitoring of movements supports the idea that, in the absence of tactile input, other sensory information is responsible for the activation of these areas. Our experimental paradigm allowed contribution of visual and muscle spindle afferents to the dexterity network. However, as it has been shown in previous studies, when joints and skin are anaesthetized, leaving only muscle afferents for proprioception, detection of the fingers position is impaired (Gandevia and McCloskey, 1976; Gandevia et al., 1983). We can therefore expect a minor impact of proprioception by muscle spindle afferents when, as in our study, the subjects compress a slender spring with anaesthetized fingers.

In the present study motor performance was relatively preserved in presence of vision but, as we show here in a pilot subgroup of subjects, was not possible without vision: the spring flipped out of their hand when trying to compress it. It has been demonstrated in behavioral and modeling studies (Jenmalm et al., 1999, 2000; Jenmalm and Johansson, 1997; Venkadesan et al., 2007) that in the absence of tactile input vision plays a compensatory role. When a slender spring, fixed to the table, was compressed by the thumb (Venkadesan et al., 2007), presence of vision resulted in greater improvement of performance when tactile information was not present. Jenmalm et al. have studied adaptation of fingertip forces to a stable object's shape and curvature. Digital anesthesia caused little impairment of grip force control when the subjects could see the objects, but performance was severally impaired without vision and somatosensory input (Jenmalm et al., 1999, 2000; Jenmalm and Johansson, 1997).

There is also evidence that vision can activate the dexterity network in the absence of the tactile input. Neurons in the intraparietal cortex, an important part of the dexterity network, have multisensory input and respond both to somatosensory and visual stimulation (Colby and Duhamel, 1991; Galletti et al., 1996; Marconi et al., 2001; Mishkin and Ungerleider, 1982). It has been shown that the inferior parietal cortex receives connections from the visual cortex and sends the efferents to the frontal cortex (Mishkin and Ungerleider, 1982), where the motor cortices, which also constitute an essential part of the dexterity network, are situated. Moreover, the dorsal premotor cortex is one of the most important targets for the intraparietal cortex, as it has been shown during visual control of movements in monkeys (Marconi et al., 2001). Normally this area receives a combination of somatosensory and visual information from the medial intraparietal area for the guidance of arm movement (Colby and Duhamel, 1991; Galletti et al., 1996). The dorsal premotor cortex, involved in movement preparation, contributes in turn to the activation of the contralateral somatosensory cortex, thus supporting corrective movements.

Consequently one can state that in the absence of the tactile input vision plays a profound role for the activation of the dexterity network and for performance of the task. And this compensatory role of vision has been reported for this task (Venkadesan et al., 2007).

3.2. *Why is there an increase in the brain activity after anasthesia?*

Peripheral deafferentation of parts of the body of the adult mammalian leads to the rapid (minutes to hours) reorganization of the somatosensory cortex (Chen et al., 2002). As a result, the cortical representation of the deafferented body part is occupied by representation of neighboring body areas. The main mechanism proposed to explain this rapid cortex reorganization is unmasking of previously present, but functionally inactive connections. Another possible mechanism, the growth of new connections, would take longer (He et al., 2004).

It is shown in several studies that the excitability of the motor cortex increases after removal of tactile input from the forearm (Nowak et al., 2001, Brasil-Neto et al., 1992, 1993; Sadato et al., 1995; Ziemann et al., 1998a, 1998b). Within minutes after the loss of tactile input, motor-evoked potentials amplitude elicited by transcranial magnetic stimulation increase several-fold (Brasil-Neto et al., 1992, 1993). In a PET study an increase of regional cerebral blood flow was observed in the primary sensorimotor area bilaterally at rest after transient anesthesia of the right forearm (Sadato et al., 1995).

Interestingly, in a previous fMRI study, more cortical activity of the dexterity network was observed when less tactile information (in the form of smoother contact surfaces for the springs) was provided during a spring compression task (Talati et al., 2005). However, changes in surface roughness induce changes in the nature of the tactile sensation that are likely very different to the effects of removing all tactile input.

One can speculate that the increase in excitability after tactile deprivation is not restricted to the primary sensorimotor area. Tight connectivity patterns between somatosensory cortex, premotor cortex and dexterity network in general provides the ground for synchronization of excitation changes between these areas. Increased cortical excitability combined with the presence of the on-line visual information and higher dexterity requirements without tactile input might therefore constitute the mechanism underlying the elevation of the activity in the premotor cortex after disruption of tactile input. This is a possible explanation for the results of our study.

3.3. *Dorsal premotor cortex*

Involvement of the dorsal premotor cortex has been shown in different contexts when the performance of the motor task is difficult for the subject. The reason for the task difficulty could be a neurological deficit (Bestmann et al., 2010; Konrad et al., 2002; Samuel et al., 1997; van Nuenen et al., 2009) or a large complexity of the task (Catalan et al., 1998; Sadato et al., 1996; Winstein et al., 1997). Stronger activation in the dorsal premotor cortex was also observed in patients with chronic stroke who had experienced substantial motor recovery such as improved hand function (Fridman et al., 2004; Johansen-Berg et al., 2002; Seitz et al., 1998; Weiller et al., 1992).

Since compensatory activation of the dorsal premotor cortex is persistently found under different circumstances, e.g. disease and performance of complex tasks, its engagement could reflect the general demand for additional support during performance of motor tasks difficult for the subject. It might, for example, reflect a general shift from automatic to more conscious planning of movements. We could also speculate that during memory-based sensorimotor transformation, the incoming sensory information would engage motor programs formed under more favorable conditions.

3.4. *Are there adaptations on the different levels of the central nervous system?*

According to a hierarchical view of motor control (Kawato et al., 1987; Loeb et al., 1999; Konen and Kastner, 2008) dexterous manipulation capabilities, such as the compression of an unstable spring prone to buckling, are likely not exclusively controlled by the neo- and somatosensory cortices (Lawrence et al., 2014; Lemon, 1993; Schieber, 2011) but involve also subcortical and spinal structures (Lawrence et al., 2014). Even if we presume a limited role of the spinal cord in movement generation in humans, the spinal cord can certainly shape the motor commands coming from supraspinal structures by gating, inhibiting, or disinhibiting the behavior of spinal circuitry (Pierrot-Deseilligny and Burke, 2005). Dynamic manipulation tasks (such as spring stabilization) occur at time scales for which spino-cortico-spinal delays would compromise closed-loop control. Neuroanatomists and electrophysiologists since the time of Sherrington have sought to map the circuitry in the spinal cord (Pierrot-Deseilligny and Burke, 2005) to understand such short-latency spinally-mediated excitation–inhibition mechanisms that enable voluntary function. These ideas were supported in previous studies where the spring compression task was employed (Mosier et al., 2011, Lawrence et al., 2014). Mosier et al. (2011) found that the level of instability achieved showed a strong association with increase in the BOLD signal in basal ganglia and in the cerebellar–parietal network. Lawrence et al. (2014) showed that spinal circuits are likely heavily involved in the regulation of instabilities during spring compressions. In the present study these findings are extended: activity was revealed in the basal ganglia, both with and without tactile input. In addition, performance of the task on a lower force level in the lack of major changes in the forebrain dexterity network during loss of tactile input strongly suggests adaptations at the level of spinal circuitry. Future studies of cortico-subcortico-spinal connectivity and spinal excitability are necessary to disambiguate interactions across hierarchical or distributed levels of neural control for different sensory conditions and manipulation tasks.

3.5. *Potential limitations*

One of the limitations of our study can be a uniformed order of condition presentation: conditions without tactile input were always performed after conditions with tactile input. It can theoretically results in the learning effects in conditions without tactile input. However, we consider this possibility as negligible, as the subjects were trained in spring compression to reach a stable level before the first behavioral session.

Lack of learning is confirmed in the behavioral experiments performed before and after fMRI sessions: lower force is observed in the spring compression test with the tactile block, which corresponds to lower dexterity.

3.6. *Conclusions*

Our finding that all brain activity present during performance of a motor task with full access to sensory information is also present after digital anesthesia indicates robustness of the brain to acute loss of tactile input. This finding in combination with a compensatory activation of the right premotor cortex, can explain a relatively well-preserved fine motor control after acute tactile deafferentation, which is so critical to robust manipulation abilities under a variety of sensory conditions in everyday life.

Further experiments are necessary to delineate which other sensory modalities, in addition to tactile, and which other circuits, in addition to cortical, participate in monitoring of the fine motor movements performance.

4. Experimental procedures

4.1. *Subjects*

Twenty-one subjects without previous history of neurological disorders participated in the study. Two subjects were excluded from the analysis because of movement artifacts, and one subject because instructions were not followed. Eighteen subjects (20–49 years, mean age 33 years, 6 males, 12 females) were included in the final analysis. All subjects were right-handed, handedness was tested with the Edinburgh Hand Inventory. The Ethical Committee of the Karolinska Hospital (Stockholm) approved the study, and all subjects gave informed consent.

4.2. *A spring compression task*

A spring compression task was employed under two sensory conditions: with and without local anesthesia to the thumb and index finger. Validity of the spring compression task as an instrument to measure dexterity has been shown in several studies (Valero-Cuevas et al., 2003; Dayanidhi et al., 2013; Pavlova et al., 2014). Subjects were placed in a supine position in an MR scanner. Subjects used low forces (below 300 g) of the thumb and index finger to compress a compliant, MR-compatible non-ferromagnetic spring of stainless steel (Fig. 1A). Because the instability of the spring increases as it is compressed, reaching and holding for 15 s the maximal level of compression (just before buckling or pressing all coils together) is indicative of the maximal level of instability the nervous system can control. The subjects could observe their hand during the task via a mirror. Two types of instructions to the subjects were given via headphones: 1) compress the spring as far as possible and hold the compression (instruction I); 2) lie still while simply holding the spring without compressing it (instruction II).

4.3. *Experimental design*

During data acquisition, 10 cycles of spring compressions were performed for each sensory condition (i.e. with and without local anesthesia). Every cycle consisted of 5 s of verbal instruction I, 15 s of sustained spring compression, 5 s of verbal instructions II and 15 s of rest (Fig. 1B). Conditions with full sensory control always preceded those with cutaneous anesthesia.

4.4. *Digital anesthesia*

The patient table of the scanner was pulled out, while the subject remained in the same position and was instructed to avoid displacement of the head. A digital nerve block was applied by injection of Lidocaine, (*2-(dietylamino)-N-(2,6-dimetylfenyl)acetamid*) at the base of the index finger and the base of the thumb on the right hand. The motor nerves to the muscles used to perform the task remained unaffected throughout the trial. Total loss of sensation (touch, pressure and nociception) of the fingertips was tested and confirmed before the second part of the experiment. This procedure took about 15 min.

4.5. *Fingertip forces*

Fingertip forces (Fig. 1B) were recorded by two miniature compression load cells (ELFF B4-10L, Measurement Specialties, Hampton, VA) mounted on the spring endcaps and a representative force time series was created based on an average of the measured index finger and thumb force time series using a custom MATLAB© program (Mathworks, Natick, MA). These forces are used as dexterity measure, for details see Dayanidhi et al. (2013). The fingertip forces were captured in separate sessions outside the MR scanner using a mock MR scanner under the same conditions as in the fMRI experiment. The participants were lying supine in the scanner with the MR coil around their heads while they observed their hand via a mirror). Initial 10 min training was allowed, which led to a stable performance. Fingertip forces were measured first with full sensation before the recordings in the MR scanner. Second, fingertip forces were measured after the MR recordings were completed and while the fingers were still anesthetized. Ten cycles of compressions were recorded in each session. A subset of subjects ($n=6$) were asked to try to perform the task with closed eyes when the fingers were anaesthetized.

As no further learning was expected after the initial training (Venkadesan et al., 2007), and as conditions of the task performance were very similar in the mock and real scanners, we extrapolated the data obtained in these behavioral experiments to the performance during MR scanning.

4.6. *Brain imaging*

Whole-brain imaging was conducted on a 1.5T scanner (Sigma Excite, GE Medical Systems, Milwaukee, WI, USA) equipped with an eight-channel head coil. First, a high-resolution three-dimensional spoiled gradient echo T1-weighted anatomical image volume was collected (voxel size $1\times1\times1\ \text{mm}^3$). Then functional images were collected using a gradient-echo, echo-planar (EPI) T2⁎weighted sequence with blood oxygenation level-dependent (BOLD) contrast (Logothetis, 2001). The following scanning parameters were used: echo time (TE)=40 ms, field of view (FOV)=22 cm, matrix size=64×64, flip angle=90°, repetition time (TR)=2.5 s. Twenty-nine continuous axial slices of 5-mm thickness were collected in each volume.

fMRI data were collected in four separate runs. Between the first two runs and the second two runs local anesthesia of the first and second digit was performed. For each run a total of 160 images were collected. The total duration of each run was 410 s, which corresponded to 10 spring compression cycles. To allow for equilibration effect, four “dummy” volumes were scanned, but not saved, at the beginning of each run.

4.7. *Data analysis*

Behavioral data were analyzed in a MATLAB© program. We identified the sustained compression phases based on the compression force magnitude and rate of change (i.e., first time derivative of force). We defined the sustained compression phase as the period of time during each hold attempt for which the force rate was bounded within one standard deviation of the mean force rate. The start was identified when the rate was close to zero and the end when the rate went out of bounds and the force dropped towards baseline. As in previous studies by Venkadesan et al. (2007) and Dayanidhi et al. (2013), the mean of the force during the sustained compression was calculated for all the hold attempts for each subject. Mean force values and standard deviations (SD) were calculated for each plateau period separately for two fingers and averaged thereafter. After this, means over all plateaus were obtained for each sensory condition for each individual.

The fMRI data were processed and analyzed in SPM8 (Welcome Department of Imaging Neuroscience, London, UK). The fMRI volumes were realigned, co-registered to each individual's anatomical T1-weighted image, segmented, normalized to the Montreal Neurological Institute (MNI) template brain and spatially smoothed with an isotropic Gaussian filter of 8 mm full-width-at-half-maximum (FWHM).

We estimated the task specific effects using the general linear model (GLM) (Worsley and Friston, 1995). Periods, when the spring was compressed (15 s), as well as rest periods (15 s) were entered as regressors into the model, separately for each run. Six movement parameters from each run, representing six degrees of freedom, were modeled to reduce the effect of the head displacement. Periods of verbal instructions (5 s) were also included as regressors and thereafter disregarded in the analysis. A 128-s high-pass filter was used to remove signal drifts. Canonical hemodynamic response function was employed in the model.

Fixed-effect analysis was performed to delineate the significant activations on the individual level. The significance of the condition-specific effects was assessed using t-statistics for every voxel of the brain to create statistical parametric maps. Two linear contrasts in which the tactile condition was contrasted to the corresponding rest were created: 1) Compression(T)–Rest(T) and 2) Compression(noT)–Rest(noT), where T and noT stand for conditions with and without tactile input, respectively.

A second-level random effect analysis was then done to allow inferences on the group level. Full factorial design with the factor Compression with two levels was used. Individual images from the fixed-effect analysis were entered for each level. Change in force between two conditions (recorded during spring compressions outside the MR camera) was entered as a covariate. Four contrasts were created: 1) Compression(T)–Rest (T) and 2) Compression (noT)–Rest(noT); 3) Compression(T)–Compression (noT) and 4) Compression(noT)–Compression(T).

To reveal the overlap in brain activity in two sensory conditions, we conducted a “minimum statistic compared to the conjunction null” analysis (Nichols et al., 2005) in SPM5 (option Conjunction). Correction for multiple comparisons on a cluster level (FWE, $p<0.05$) was used to control for false positives.

Labeling of the activation regions was done with the help of the SPM anatomy toolbox (Eickhoff et al., 2005) and probability maps from Mayka et al. (2006).

Conflict of interest statement

Francisco J. Valero-Cuevas holds US Patent no. 6,537,075 on some of the technology used, but has no active or pending licensing agreements with any commercial entity. All other authors report no conflicts of interest.

Acknowledgments

We acknowledge Rita Almeida for consulting in statistical analysis. The work is supported by Promobilia, ALF and

Norrbacka-Eugenia foundations, Swedish Research Council (5925), Swedish Brain Foundation, Swedish Foundation for Strategic Research, Berzelii Center Stockholm Brain Institute (Vinnova & Swedish Research Council), Strategic Neuroscience Program at Karolinska Institutet and Foundation Frimurarna Barnhuset. Research reported in this publication was supported in part by NIAMS of the National Institutes of Health under award numbers R01AR050520 and R01AR052345 Grants to FVC. The content is solely the responsibility of the authors and does not necessarily represent the official views of Karolinska Institute or the National Institutes of Health.

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