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Challenging the brain: Exploring the link between effort and cortical activation

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Abstract

To better understand the contributions of effort on cortical activation associated with motor tasks, healthy participants with varying capacities for isolating the control of individual finger movements performed tasks consisting of a single concurrent abduction of all digits (Easy) and paired finger abduction with digits 2 and 3 abducted together concurrently with digits 4 and 5 (Hard). Brain activity was inferred from measurement using functional magnetic resonance imaging. Effort was measured physiologically using electrodermal responses (EDR) and subjectively using the Borg scale. On average, the Borg score for the Hard task was significantly higher (p=0.007) than for the Easy task (2.9±1.1 vs. 1.4±0.7, respectively). Similarly, the average normalized peak-to-peak amplitude of the EDR was significantly higher (p=0.002) for the Hard task than for the Easy task (20.4±6.5% vs. 12.1± 4.9%, respectively). The Hard task produced increases in sensorimotor network activation, including supplementary motor area, premotor, sensorimotor and parietal cortices, cerebellum and thalamus. When the imaging data were subdivided based on Borg score, there was an increase in activation and involvement of additional areas, including extrastriate and prefrontal cortices. Subdividing the data based on EDR amplitude produced greater effects including activation of the premotor and parietal cortices. These results show that the effort required for task performance influences the interpretation of fMRI data. This work establishes understanding and methodology for advancing future studies of the link between effort and motor control, and may be clinically relevant to sensorimotor recovery from neurologic injury.

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1. Introduction

Motor task performance is often associated with levels of effort that match the levels of task challenge. In the past, effort sense has been defined as the perception of a command passed to an active muscle used to estimate the level of force production for a given task (Gandevia and McCloskey, 1977b). This awareness of the effort required to activate a muscle was thought to be centrally driven; involving, but independent from peripheral contributions (Gandevia and McCloskey, 1977a).

In parallel, motor task performance is characterized by activation across a broad network of brain regions. This network has been elucidated in studies assessing cortical activity associated with, for example, intermittent power and precision grips (Kuhtz-Buschbeck et al., 2008), static and dynamic hand movements (Thickbroom et al., 1999), and single versus multiple finger movement (Remy et al., 1994). In each of these examples, precision and fine motor control have been contrasted against gross movements, which may be one way to assess the level of effort required to accomplish the required task.

While the link between motor output and effort has been established and the cortical network for motor output identified, the exploration of the neural correlates of effort has been a more complex undertaking. The reason for this is that it is difficult to dissociate the neural correlates of effort from those involved in motor control. Indeed, the term “effort” can be linked to numerous components of motor control processes, each with their own mediating factors and unique cortical substrates. For example, effort can be linked to increases in volitional force production, which is associated with increased activation in sensorimotor cortical areas in isometric gripping paradigms (Dettmers et al., 1995; Dai et al., 2001). Alternatively, effort could also refer to perceived difficulty in sequential task patterns. Accordingly, the influence of task complexity or coordination on cortical activation during sequential tapping sequences have been identified (Wexler et al., 1997). As another example, effort could be associated with muscle fatigue, which has shown to increase cortical activity with a concomitant decrease in EMG and a reduced capacity to volitionally activate muscle (Sehm et al., 2009). It should be noted that while it may be attractive to consider muscle fatigue an appropriate model for assessing effort, the potential involvement of peripheral factors in fatigue (for review see Gandevia, 2001) could confound the interpretation of the link between cortical activity and effort. In addition, the potential link between effort, cortical activity, and fatigue becomes even more complex when one considers that the patterns of cortical and muscle activation vary with the type of protocol used to induce fatigue (Liu et al., 2002, 2003, 2005).

When associated with neurological injury (i.e. stroke), alterations in effort sense pose an additional challenge to understanding the neural correlates of effort. Individuals with neurologic injury who struggle to execute a movement compromised by injury display altered, disproportionately high levels of effort (Gandevia, 1982) and it has been hypothesized that the return of appropriate effort sense is partially responsible for motor recovery in stroke patients following specific types of rehabilitation (Sunderland and Tuke, 2005). This is particularly relevant to individuals with specific neurological disorders who report that more effort is required to perform a task even though the actual level of force output associated with the task is low or non-existent (Brodal, 1973; Rode et al., 1996). Imaging studies have also identified unique patterns of cortical activation post-stroke (for review, see Cramer, 2008), thought to reflect disproportionate levels of effort during motor task performance. While fatigue may contribute to effort sense in individuals with multiple sclerosis (Thickbroom et al., 2006), Riley and Bilodeau (2002) indicate that during a fatiguing task, paretic muscles of patients following stroke may not be sufficiently activated to induce fatigue.

The features linking task challenge and effort are: (1) high relative levels of force/load, reflecting the challenge of generating sustained or near maximal levels of force and (2) the difficulty associated with engaging specific muscles, reflecting the challenge of coordinating muscle activity (Fig. 1). This model emphasizes the link between effort and task complexity rather than load because interaction with one's environment requires adept modifications in sequencing and co-ordination. Achieving adequate levels of force may be considered a secondary requirement. Recent evidence identifying a cortical network in frontal and parietal areas linked to motor output of the index finger that is independent of the level of EMG (van Duinen et al., 2008) supports the possibility that cortical areas for muscle force are dissociable from other features of motor control.

The current work set out to test an approach for exploring the influence of effort linked to the challenge of isolating the control of individual muscles in healthy adults. In this population, the acquisition of new skills requires high levels of cognitive effort (Oliveira and Goodman, 2004); however, a model of testing based on task novelty (and learning) is a difficult protocol to employ due to the rapidly changing state of individuals as learning progresses. Individuals also demonstrate considerable variability in the capacity to isolate and perform specific motor activities involving the hands and face (i.e. movement of a finger joint, raising an eyebrow). These differences are most likely attributable to inherent differences in CNS connectivity. It is proposed that the struggle faced by those who cannot easily perform specific isolated finger movements will be characterized by elevated levels of effort and increased cortical activation and that the objective index of person-specific effort can be used to better reveal this effort related increase in cortical activity. While the eventual aim is to address such factors in a patient population, the present study focuses on healthy individuals to investigate the relationship between effort and brain activation using functional magnetic resonance imaging (fMRI).

2. Results

2.1. Overall task differences

The initial comparisons were conducted by contrasting the performance of the two tasks (Easy and Hard; Fig. 2) within all participants tested. Differences in subjective and objective measures of effort were different between the two tasks. On average, participants rated the Easy task to be 1.4±0.7 on the Borg scale and the Hard task to be 2.9±1.1 on the Borg scale

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(*p*=0.007). In addition, the average normalized peak-to-peak amplitude of the EDR measures was 12.1±4.9% for the Easy task and 20.4±6.5% for the Hard task (*p*=0.002). It is noteworthy that phasic EDRs were recorded for individual single movements permitting the measurement of autonomic responsiveness linked to each single movement event. Fig. 3 depicts the normalized, transient EDR for each event.

Overall, the performance of the Easy task involved a broad network of significantly activated brain regions. Fig. 4A illustrates the group average activation, revealing that bilateral supplementary motor area (SMA), premotor, sensorimotor, and parietal cortices, putamen, and cerebellum were activated during the performance of the Easy task. The areas of statistically significant activation associated with performing the Hard task were the same as those involved in the performance of the Easy task with the addition of the thalamus and superior parietal lobule (BA7), bilaterally, left precentral gyrus (BA6), and right middle frontal gyrus (BA10). In addition, the performance of the Hard task was also associated with an increase in the number of activated voxels in several areas (Fig. 4B). Comparing the specific regions of interest between the tasks (i.e. Hard-Easy contrast) revealed significantly greater activation in the left superior temporal gyrus (BA 22) and inferior parietal lobule (BA 40), right precuneus (BA 7), middle frontal gyrus (BA 10) and the cerebellum, bilaterally. These findings are depicted in Fig. 4C and the average Talairach coordinates and voxel counts are reported in Table 1.

Even though the force requirements for these tasks were low, EMG analysis conducted on task performance outside of the scanner was used to determine if task performance (Easy and Hard) was distinguished by different amplitudes of contraction. Analysis of the normalized iEMG data revealed no differences in activation of the ED and ADM muscles between tasks, as well as task-dependent differences in activation of the dorsal interossei muscles (Fig. 5). As reported in Table 2, the activation ratio of the ED for both tasks was greater than for any other muscle. However, there was no statistically significant difference between tasks. The EMG measures for ADM did not differ between tasks. The difference in the mean $iEMG_{burst}$:$iEMG_{pre}$ ratio for the FDI was small (1.31±0.73), but significantly greater for the Easy task as compared to the Hard task (*p*=0.035). Conversely, the iEMG ratio for the 2DI was significantly greater for the Hard task as compared to the Easy task (*p*<0.001). The magnitude of the iEMG ratios for the FDI and 2DI muscles was comparable to that of the ADM muscle. Table 2 reports the mean iEMG ratios for all muscles.

2.2. Analysis of subgroups based on effort measures

2.2.1. Subjective index of effort (Borg scores)—As expected, there was variation in the reported degree of effort across subjects. Whereas all participants rated their perceived exertion to be below 3 (moderate) on the modified Borg scale during the performance of the Easy task, five participants reported Borg scores that were only one increment higher for the Hard task (2.2±1.3 vs. 1.6±0.9 for Hard and Easy, respectively). The other six participants reported Borg scores that were at least two increments higher for the Hard task (3.5±0.5 vs. 1.2±0.4 for Hard and Easy, respectively). The average Borg score for the Hard task in this subgroup of six was significantly higher than the average Borg score associated with the Hard task in the subgroup of five participants (*p*=0.004), further emphasizing the subject-specific differences in task difficulty. This is consistent with anecdotal observations that some participants found the Hard task to be much more difficult than others. On the basis of the Borg scores, a subgroup comparison was conducted between those who found the Hard task more difficult (ΔBorg score>2, Hard-Easy, n=6) and those who found it relatively easy (ΔBorg score<2, Hard-Easy, n=5). Subdivision of the fMRI data by groups based on Borg score showed significantly greater activation in the left pre- and post-central gyrus (BA 4 and 3, respectively), middle occipital gyrus (BA 37), inferior parietal lobe (BA 40), right lingual gyrus (BA 17) and extrastriate cortex, bilaterally (BA 18, 19), the prefrontal cortex (BA 10 on the right and BA 46, 47 bilaterally) and cerebellum bilaterally for those participants who found the hard task more difficult. Table 1 shows the voxel counts for the ROIs implicated in this contrast.

2.2.2. Objective measure of effort (electrodermal responses)—Task complexity was further assessed by separating the participants based on the differences in mean peak-to-peak amplitude of the EDR (ΔEDR) between the Easy and Hard tasks. Six participants produced EDR change values (Hard–Easy task) of >7.0% (mean: 12.4±5.7%). It is noteworthy that four of these six participants were the same as those having a >2 point Borg score difference. The differences in classification using the Borg scale compared to the EDR amplitude underlines the importance of using a more objective measure of effort related to autonomic responses that is recorded as a continuous variable, rather than relying on self-reporting of effort using an ordinal scale. One participant was classified as having a change score on the Borg >2, but a change score in EDR of approximately 0. Another participant perceived both tasks to be equally easy and gave both tasks a Borg score of 1, yet revealed a ΔEDR value of 9.7%. The remaining five participants had ΔEDR values of <7.0% (mean: 3.2±3.1%) that were significantly lower than those of the remaining participants (p=0.01). The rationale for creating subgroups based on ΔEDR value was the possibility that the self-reporting (using Borg scores) may have under- or over-estimated the “true” level of effort. Overall there was a significant relationship between reported Borg scores and EDRs assessed across all participants (Fig. 6, R^2=0.46, p<0.0005).

All areas that were shown to be active using Borg-based contrasts were also active when the data were separated by EDR differences except for the left post central gyrus (BA 3), right lingual gyrus (BA 17) and right inferior frontal gyrus (BA 47). The separation of data by EDR-based contrasts demonstrated additional activation of the left middle frontal gyrus (BA 10), left striate and right extrastriate cortices (BA 17 and 18, respectively), left superior temporal gyrus (BA 22), left inferior parietal lobule (BA 40), right medial frontal gyrus (BA 6), and postcentral gyrus, bilaterally (BA 5). These regions were not observable in the Borg-based separation of the data (Table 1).

3. Discussion

The purpose of this study was to examine the influence of the effort associated with motor task performance on brain activity in healthy adults. Increasing task challenge elicited generalized increases in the fMRI BOLD response across the motor network, enabling visualization of additional cortical recruitment. Contrasting participants based on a subjective index of effort (Borg scores) revealed greater activity in the network involved in task performance in the subgroup of participants that found the Hard task more difficult. The extent of brain activity was more apparent when subgrouping was based on a physiological index of effort using EDR measures. These results emphasize the importance of using indices of effort to probe individual differences that are subjectively perceived and objectively measurable to better understand the influence of effort on task performance.

3.1. Indices of effort

The Borg scale was used as a subjective self-reporting tool that allowed individuals to rate their perceived effort during task performance (Borg, 1982). The Borg scale is easy to implement and, in this study, was able to better differentiate task-related differences than labeling the tasks as ‘hard’ and ‘easy’ alone; yet, it may have been susceptible to factors unrelated to actual task differences. Typically, participants are required to rate their exertion during a task (Williamson et al., 1999), but in the present study, perceived effort was gauged at the end of the trial. This may have influenced their perception of task challenge. Alternatively, their responses may have been influenced by the “better-than-average” effect observed in social psychology where participants describe themselves more positively than others (Alicke et al., 1995).

The objective physiologically-based measure of effort was the EDR, a measurement of changes in the electrical conductance of the skin caused by activity of the sweat ducts as a consequence of sympathetic nerve activity (Lim et al., 2003) that provides a measure of autonomic response from which effort sense can be inferred. The extent of scaled, task-dependent modulation of EDR amplitude observed in the present study (Fig. 3) suggests that EDR measurement can be an attractive tool for assessing the extent to which learning effects, fatigue, or attentional changes confound other measures of performance. If the changes in brain activation observed with fatigue (Liu et al., 2002, 2003, 2005) and attention (Johansen-Berg and Matthews, 2002; Binkofski et al., 2002) and the changes in cortical excitability observed with learning (Perez et al., 2004) are all influenced by effort, then the quantification of effort can be used to facilitate understanding of the interaction between task performance and the underlying physiological processes.

The observation that subjective and physiologic measures of effort provided contextual information for interpreting task performance in excess of what was gleaned from task performance alone was not inconsequential. Despite this, the relationship between measures was moderate. Four of the six participants with high change scores in the Borg measure were classified as having high EDR change scores. The discrepancy between measures in some individuals could have been due to the ordinal nature of the Borg scale, whereas the EDR was measured as a continuous variable. These observations may be interpretable as examples of differences in precision between perceived and physiologic measures of effort. One participant displayed equally high EDR amplitudes for the Hard and Easy tasks despite reporting differences in Borg score. Another participant reported no difference in Borg score between tasks despite demonstrating differences in EDR amplitudes. The finding that the brain activation pattern was more profoundly distinguished when comparing groups based on EDR, suggests that the physiologic index may have the ability to characterize the link between effort and the underlying task challenge more directly. This is consistent with studies reporting improvements in modeling cortical responses during the performance of sensorimotor tasks when the EDR was used in both univariate and multivariate statistical models (MacIntosh et al., 2007).

3.2. Influence of task challenge on fMRI and EMG

There is evidence of an association between increased force production and augmented cortical activity (Thickbroom et al., 1998; Dai et al., 2001). The observations that, in patients, force output covaries with activity in the contralesional premotor cortex and that the relationship between force output and ipsilesional motor cortical activity weakens with higher levels of damage to the corticospinal system (Ward et al., 2007) also support this relationship. However, we do not believe that changes in force production accounted for the task-related difference in the present study. Characterization of the electromyographic responses during the performance of the Hard and Easy tasks in the present study revealed no differences in the activation profiles of the ED and ADM muscles and significant differences for the FDI and 2DI muscles. The FDI produced slightly greater activity during the Easy task, arguing against the possibility that the fMRI signal differences between the Hard and Easy task were simply the product of greater intensity of muscle activation. Because the differences in iEMG between tasks were small for the FDI and 2DI and not significant for ED and ADM, the net EMG activation for all muscles was relatively constant between tasks. Thus, any differences in EMG could be attributable to the isolation/ recruitment of muscles that was task specific.

If increased effort evolves from challenges in isolating individual digit control and not due to elevated force production, the question that arises is: what is the source of the task-related increases in cortical activity? One possibility is that the Hard task relied on somatosensory information from proprioceptive and/or cutaneous receptors for successful completion of the task. Presumably, this feedback would be required for precision in movement, especially for tasks such as this that would likely be considered to be novel or complex. Activation of the bilateral parietal and pre-frontal areas as well as the rostral cingulate and ventral pre-motor areas during a precision gripping task (Ehrsson et al., 2000) support this hypothesis. The similarities between the activation patterns depicted in this study and those depicted by Kuhtz-Buschbeck and colleagues (2001) during a precision-gripping task lend further support to the idea that the activation patterns observed in the Hard task were related to task complexity. It is also possible that the Hard task required some level of visuo-spatial processing in excess of what was required for the Easy task. For example, activation of BA40 has been associated with imitation of finger configurations (Tanaka and Inui, 2002). It has been suggested that it is the complexity of the required arrangement of the fingers that contributes to this activation (Muhlau et al. 2005). In light of this proposed requirement, it is suggested that the increases in effort may be associated with increased attentional load during task performance driven by online processing of feedback during task performance.

In healthy individuals, attention to the presence and location of sensory stimuli can cause changes in the interaction between sensory inputs and motor output (Rosenkranz and Rothwell, 2006). Such increases in attentional demands may also be the foundation for network-wide increases in cortical activation seen in complex motor tasks (Rao et al., 1993;

Remy et al., 1994; Wexler et al., 1997). The salient feature of the present work is that it is possible to see such network-wide facilitation in tasks that feature low levels of force and less complex sensorimotor transformations but are associated with elevated levels of effort. The underlying theme is that tasks that are difficult to perform and that require elevated levels of attention and precise feature extraction for successful completion all require increased cortical processing. This is in contrast with those tasks which are simple to perform and can be thought of as familiar and require relatively low levels of cortical activity. This dichotomy bears striking resemblance to the differences in phenotypes of individuals with and without changes in effort sense as described in the literature (Brodal, 1973).

It should be noted that this study is limited by the absence of concurrent EMG recordings while participants were in the scanner, the absence of EMG recordings from the contralateral hand, and the absence of EMG recorded from additional ipsilateral muscles. Without these measures, the possibility that the observed differences in cortical activation were associated with a spread in muscle activation (Dettmers et al., 1995) or mirroring (Sehm et al., 2009) rather than differences in effort cannot be ruled out. However, in the absence of concurrent measures of cortical activity, evidence from the four muscles from which muscle activity was recorded outside of the scanner supports the concept of increased task complexity without a concomitant increase in task load. In addition, evidence demonstrating increased activation with lower levels of force (i.e. precision grip; Ehrsson et al., 2001) or activation during finger movement not correlated with force (Dettmers et al., 1995) indicates that factors other than increases in muscle force can contribute to increased activation in regions of the motor network.

3.3. Applicability to motor recovery of individuals with neurologic injury

The task used in the present study is not specifically useful for assessing sensorimotor recovery in patients with neurologic injury, as the ability to perform the task on the affected side is dependent upon the severity and location of the injury. Despite this, the concept of a dissociation between motor output and effort is relevant and worth additional study. The effortful task employed here was developed with the goal of mimicking simple motor tasks associated with an exaggerated effort sense reported by individuals following stroke (Brodal, 1973). It has been documented that the integrity of the internal capsule is linked to effort sense (Rode et al., 1996) and sensorimotor recovery following stroke (Werring et al., 1998). From this perspective, awareness of the motor command remains intact; the impairment lies in the execution of the command. Patients also demonstrate increased activity in primary and secondary motor areas that is thought to reflect the recruitment of available neurons to compensate for the loss of function (Feydy et al., 2002). However, the suggestion that recruitment of secondary motor areas leads to less efficient motor output (Ward et al., 2007) indicates that the mismatch between effort and motor output is functionally relevant. The decrease in cortical activity during recovery, which may be indicative of changes in attentional demands or neuronal reorganization (Ward et al., 2003), may parallel changes in perceived and/or physiologic-indices of effort. Initial studies demonstrating links between EDR and BOLD responses in patients show the putative value of using these techniques to assess recovery following neurologic injury (MacIntosh et al., 2008).

This study has demonstrated that subjective and physiologic measures of effort are useful for identifying task-dependent differences in brain activation. Objective, physiologic measures are particularly valuable for interpreting behavioural data. These findings can improve the understanding of behavioural measures of recovery following acquired neurologic injury by accounting for the influence of effort on behaviour. Importantly, this work also provides methodology for advancing future studies of the specific mechanisms by which increased sense of effort influences control of movement and the recovery from neurologic injury.

4. Experimental procedures

4.1. Participants

Seventeen participants (11 females, 6 males, 29.1±7.8 years) with no neuromuscular deficits participated in this study. Eleven participants were involved in the main fMRI study, while the additional six participants completed the EMG portion of the study outside of the scanner. Based on self-reports, all participants were right-handed and each gave informed consent to participate. The study was conducted with approval from the Research Ethics Board at Sunnybrook Health Sciences Centre.

4.2. Tasks

Participants were presented with images of hand/finger positions at one of two levels of difficulty: 1) a single concurrent abduction of all digits (Easy) and 2) paired finger abduction with digits 2 and 3 abducted together concurrently with digits 4 and 5 (Hard, Fig. 2). Participants were then instructed to mimic each image that was presented to them and to hold the position for the 2-s period for which the image was presented. This was followed by an 18–s rest period where participants were required to keep their fingers in a neutral, relaxed position. The visual cues for the easy and hard tasks were randomized and a total of 12 events were performed for each task. Task performance was visually monitored by an experimenter. Trials that involved compensatory movements, movement performed in distinct steps, or movements that included out-of-plane finger positions (i.e. finger extension or flexion) were noted and excluded from the analysis. Upon completion of the scanning session, participants were required to rate their perceived effort for both the Easy and Hard task on a modified Borg Scale (Borg, 1982). This scale ranges from 0 to 10, with 0 indicating that the task was very easy and 10 indicating that the task was very hard. The task was performed with the dominant right hand.

The trials were repeated in an additional group of six participants outside of the scanner to characterize the electromyographic (EMG) profiles of the two tasks. The participants were seated comfortably in a chair with the dominant arm abducted and with the elbow flexed and the forearm pronated. The arm was supported by a table whose height could be adjusted to suit the individual participant. The images were presented at the same frequency and in the same order as those presented to the participants inside the scanner.

4.3. Imaging parameters

Magnetic resonance images were collected using a 3 Tesla scanner (Signa; GE Medical Systems, Waukesha, Wisconsin; NV/I platform; 12× software release) and the standard quadrature birdcage head coil. All blood oxygenation level dependent (BOLD) fMRI scans (26 Axial slices 5 mm thick; field of view (FOV)=20×20 cm; TE/TR/flip angle=30 ms/2000 ms/70°; acquisition matrix=64×64) were performed using single-shot T_2^*-weighted spiral k-space acquisition with in/out trajectory, off-line gridding, magnetic field inhomogeneity correction and image reconstruction (Glover and Law, 2001). High resolution anatomical images were obtained using spoiled gradient echo imaging (124 axial slices 1.4 mm thick; FOV=22×16.5 cm; TR/TE/angle=4.2 ms/10.1 ms/15°; acquisition matrix=256×192).

4.4. Electrodermal responses (EDR)

To provide additional characterization of behavioural performance during fMRI, electrodermal (skin conductance) responses were recorded during imaging. Prior to securing the electrodes to the fingers of the hand that was not involved in the motor task, the skin was exfoliated with an emery board and cleaned with an alcohol wipe. Electrodermal electrodes designed for fingers (Astro-Med Inc., West Warwick, Rhode Island) were filled with conductive gel and fastened to the palmar surface of the middle phalanges of the fourth and fifth digits. The skin conductance signals were pre-amplified and subsequently converted to optical signals using an fMRI-compatible customized optoelectric system (MacIntosh et al., 2007). The fiber optic cable was passed through the waveguide and converted back to a voltage signal outside the magnet room. The skin conductance measures were subsequently filtered (2 Hz low-pass cutoff frequency), amplified and digitized at 100 Hz using LabVIEW (National Instruments, Austin, Texas).

4.5. Electromyography

Task-related EMG conducted outside the scanner was recorded using bipolar surface Ag-AgCl electrodes (10 mm diameter) placed 25 mm apart on the first and second dorsal interossei (FDI and 2DI, respectively), abductor digiti minimi (ADM), and the extensor digitorum (ED) muscles of the dominant hand/arm. Prior to attaching the electrodes, the skin was cleaned and abraded. Signals were amplified (2000x), band-pass filtered (10–500 Hz), digitized at a sampling rate of 1000 Hz (Noraxon USA Inc, Scottsdale, Arizona) and stored for offline analysis.

4.6. Data analysis

4.6.1. fMRI analysis—For each scan a time series consisting of 124 images per slice location was generated by offline gridding and reconstruction of the raw data. The reconstructed time courses were analyzed using BrainVoyager QX 1.3 software (Brain Innovation, Maastricht, The Netherlands). Prior to further analysis, the first 4 volumes at each slice location were excluded to prevent artifact from transient signal changes as the brain reached a steady magnetized state. Prior to co-registration, the functional data was pre-processed by linear trend removal, temporal high pass filtering to remove non-linear low frequency drift, and 3-dimensional motion correction using trilinear interpolation to detect and correct for small head movements during the scan by spatially realigning all subsequent volumes to the fifth volume. Estimated translation and rotation measures were visually inspected and never exceeded 1 mm and 1 degree, respectively. The functional data sets were transformed into Talairach space (Talairach and Tournoux, 1988) through co-registration with spatially transformed 3D anatomical data sets for each individual subject. The resulting volume time courses were filtered using a 4 mm Gaussian kernel at full width half maximum for group level analyses.

In order to statistically evaluate the relative differences across the two experimental conditions a multiple regression approach was employed using two predictors: Easy and Hard, with the 18 s of no stimulation serving as a baseline. Two task protocols using dummy-predictors (for the predictors not included in a given run) were adopted and convolved with a boxcar haemodynamic response function (Boynton et al., 1996) to account for the expected shape and temporal delays of the physiological response. The resulting reference functions served as the model for the response time course functions used in the general linear model. Contrast maps were created using a voxel-based approach to show relative changes for Easy vs. baseline, Hard vs. baseline and Hard vs. Easy. Activated voxels were considered significant if the threshold of an individual voxel exceeded $p<0.001$ and they formed a cluster of 10 mm^3, which corresponds to a corrected threshold of $p<0.05$ (Forman et al., 1995). The center of gravity and *t*-statistics were extracted for each significant cluster. For each of the significantly activated clusters identified from the contrasts defined above, the Talairach co-ordinates for the centre of gravity, voxel counts, Brodmann areas and brain regions were obtained using the Talairach Daemon (The Research Imaging Center, UTHSCSA, San Antonio, Texas).

Secondary analyses evaluated the differences in activation during the Hard task as a function of the effort associated with performance of the task. Two groups were identified based on their scores on the difference in Borg score scale and the EDR change associated with task performance. A contrast was performed for the Hard task between those with a large difference in the Borg score between the Hard and Easy tasks (ΔBorg score>2) and those revealing little difference in Borg scores between tasks (ΔBorg score<2). A similar contrast was performed between groups with high (ΔEDR>7%) and low (ΔEDR<7%) task-related changes in EDR. In each comparison, there were 6 participants in the high effort groups and 5 in the low effort groups. Only four of the participants in the group with large differences in Borg score revealed similarly large changes in EDR, thus the groups for the secondary analyses comprised different sets of participants.

4.6.2. EDR—To allow for comparisons across participants, the EDR signals were normalized to the peak value of the EDR recording for each participant. The highest sample in the recording was given a value of 1 and the lowest was given a value of 0. The data were subsequently band-pass filtered (0.0075–0.3 Hz) removing the low-frequency drift in the signal and leaving only the transient, event-related changes in EDR amplitude. Once the data were pre-processed, the peak-to-peak amplitude of the normalized EDR was calculated for each event. Average peak-to-peak amplitude for each task was determined for each participant and reported as percent of the range of values in the EDR signal.

4.6.3. Electromyography—Analysis of EMG data collected outside the scanner was conducted for each muscle individually. The EMG activity associated with each event was aligned to EMG burst onset and averaged across the 12 events for the Easy and Hard tasks. A “burst” was classified as the EMG activity exceeding the mean+5 SD of baseline activity

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for a minimum duration of 50 ms. The magnitude of the EMG activity associated with the performance of each task was assessed by calculating the area of the EMG signal integrated over the first 200 ms of the burst ($iEMG_{burst}$). The iEMG was also calculated for the 200 ms preceding the EMG burst related to task performance ($iEMG\text{-}_{pre}$). The magnitude of muscle activity was subsequently normalized by calculating the ratio of $iEMG_{burst}$:$iEMG_{pre}$ for each event.

4.7. Statistical analysis

Statistical analyses of behavioural data were performed using SPSS v12.0 (SPSS Inc., Chicago, Illinois). Between task (Hard vs. Easy) comparisons of Borg response scores and EDR were conducted using the Wilcoxon signed-rank test and paired t-test, respectively. To dichotomize the data for contrast appropriately, the separation of the ΔBorg and ΔEDR values into two groups was based on the initial distribution of values. The ΔBorg values fell into ranges greater than or less than 2. The ΔEDR values fell into ranges greater or less than 7% of peak to peak amplitude. ΔBorg and ΔEDR group differences were assessed using a Mann–Whitney *U* test and an independent *t*-test, respectively. The difference in normalized iEMG between the Easy and Hard tasks for each muscle was assessed using the Mann–Whitney *U* test. For all analyses, a level of $p<0.05$ was considered statistically significant.

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Abbreviations

ADM	Adductor digiti minimi
BA	Brodmann area
EDR	electrodermal response
ED	extensor digitorum
FDI	first dorsal interosseous
fMRI	functional magnetic resonance imaging
EMG	electromyogram
2DI	second dorsal interosseous
SMA	supplementary motor area

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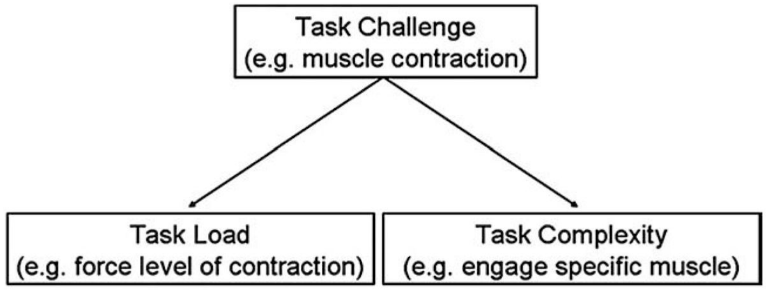

Fig. 1.

Schematic of the components of task challenge. A given motor task requires an increase in motor output to: (1) match force production to task load and (2) match effort to task complexity.

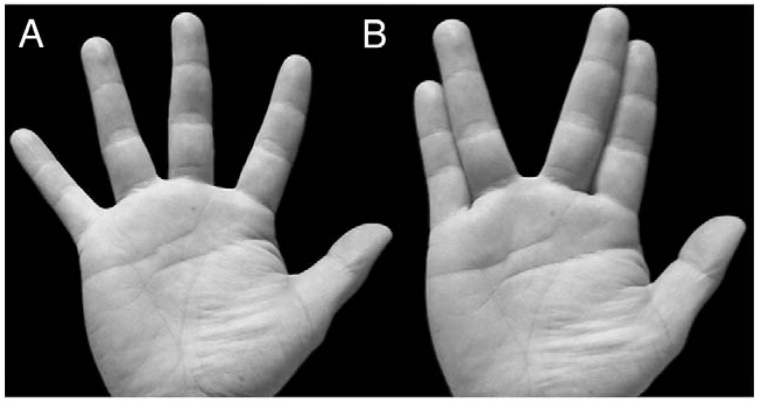

Fig. 2.
Depiction of the images associated with the tasks employed in this study: Easy (A, all fingers slightly abducted) and Hard (B, paired abduction).

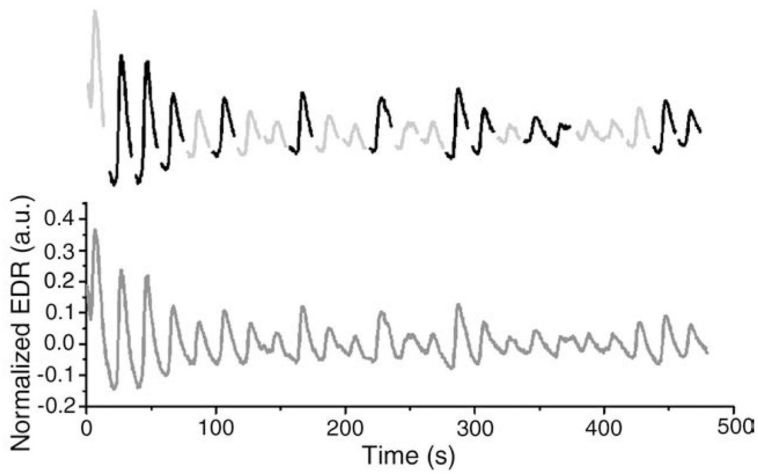

Fig. 3.
Grand average normalized EDR trace for the duration of a test session. The top panel identifies the occurrence of each event individually and depicts event-specific scaling of EDR amplitude for Easy (gray) and Hard (black) events.

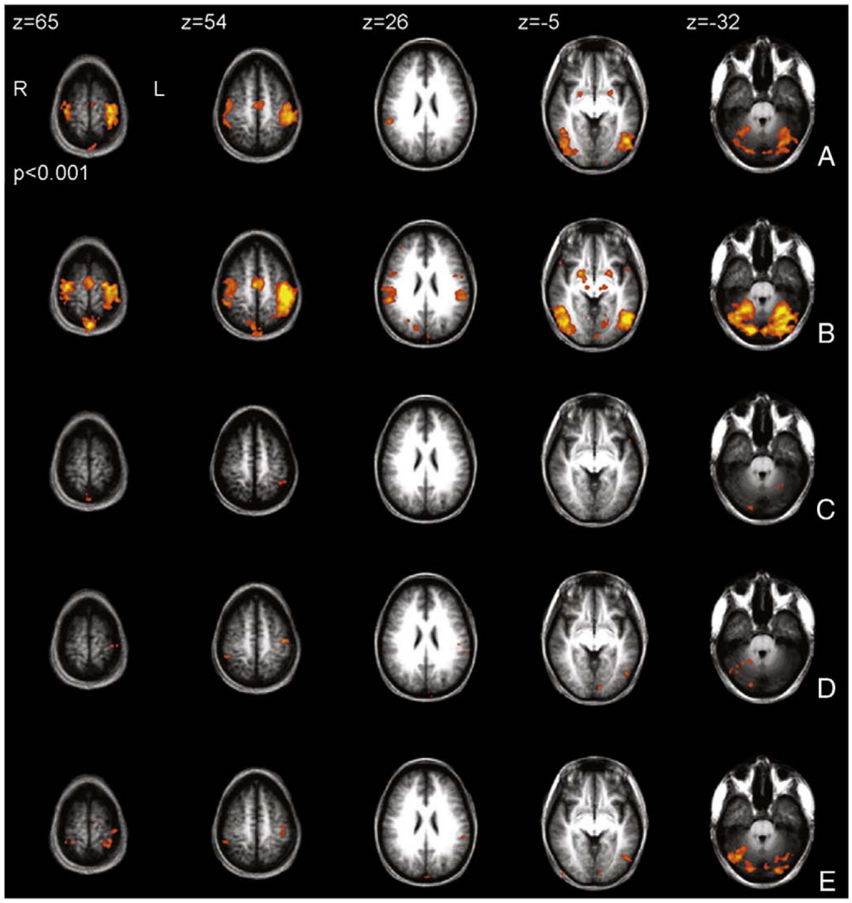

Fig. 4.

Group average activation maps for five different contrasts. (A) Easy–rest; (B) Hard–rest; (C) Hard–Easy; (D) Hard task, Δ Borg>2–ΔBorg<2; (E) Hard task, ΔElectrodermal Response (ΔEDR)>7%–ΔElectrodermal Response (ΔEDR)<7%.

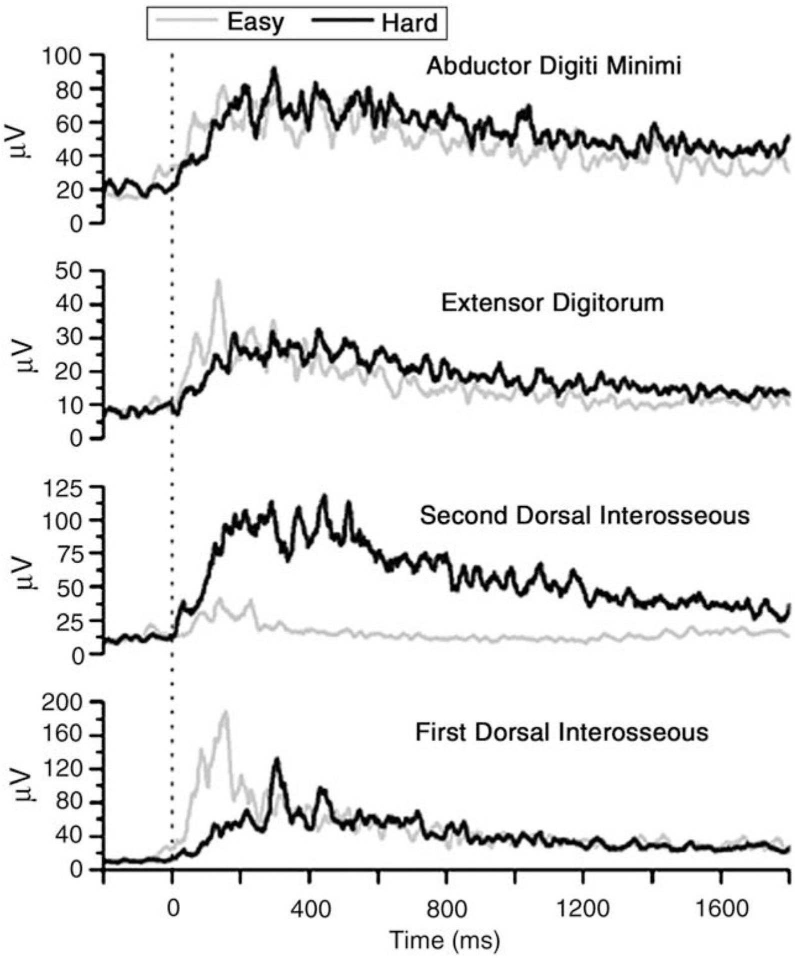

Fig. 5.

Single subject representation of the average EMG response aligned to burst onset (vertical line) associated with the Hard (black) and Easy (gray) tasks for each muscle. The data were low-pass filtered at 20 Hz for display purposes only.

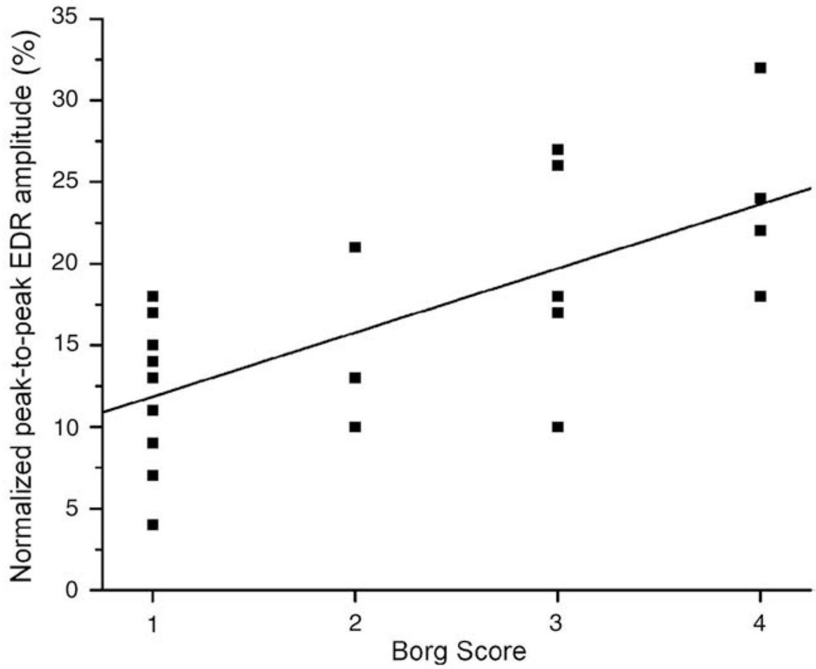

Fig. 6.
Plot of the normalized mean peak-to-peak EDR amplitude in relation to Borg score for all participants for the Easy and Hard tasks.

Table 1

Identification of regions highlighted in the contrast map of Hard vs. Easy, ΔBorg>2–ΔBorg<2 during the performance of Hard task, and ΔElectrodermal Response (ΔEDR)>7%–ΔElectrodermal Response (ΔEDR)<7% during the performance of the Hard task.

Location	**Talairach coordinates**			**Contrasts**		
				Hard vs. Easy	**ΔBorg score**	**ΔEDR amplitude**
	X	***Y***	***Z***	**Voxel count**	**Voxel count**	**Voxel count**
L parietal lobe (postcentral gyrus, BA 3)	−41	−18	56		867	
L frontal lobe (precentral gyrus, BA 4)	−38	−25	59			967
	−35	−25	68		532	
L parietal lobe (postcentral gyrus, BA 5)	−28	−43	65			1390
R parietal lobe (postcentral gyrus, BA 5)	34	−42	63			113
	23	−39	67			123
R frontal lobe (medial frontal gyrus, BA 6)	3	−27	69			565
R parietal lobe (precuneus, BA 7)	10	−77	47	370		
L frontal lobe (middle frontal gyrus, BA 10)	−26	55	10			245
R frontal lobe (BA 10)						
Middle frontal gyrus	43	63	2		117	
Superior frontal gyrus	22	67	15			201
L occipital lobe (Inferior occipital gyrus, BA 17)	−10	−91	−9			283
R occipital lobe (lingual gyrus, BA 17)	12	−86	2		125	
L occipital lobe (cuneus, BA 18)	−5	−99	19		231	
	−9	−98	6		262	
	−13	−96	7			441
R occipital lobe (cuneus, BA 18)	4	−99	3			108
L occipital lobe (BA19)						
Lingual gyrus	−20	−63	2		395	
Cuneus	−2	−93	28			372
Fusiform gyrus	−46	−77	−15			566
L temporal lobe (superior temporal gyrus, BA 22)	−51	11	−2	223		
	−50	10	−1			266
L temporal lobe (inferior temporal gyrus, BA 37)	−50	−66	−2			645

Location	Talairach coordinates			Contrasts		
				Hard vs. Easy	ΔBorg score	ΔEDR amplitude
	X	*Y*	*Z*	Voxel count	Voxel count	Voxel count
L occipital lobe (middle occipital gyrus, BA 37)	−48	−66	−5		144	
L parietal lobe (inferior parietal lobule, BA 40)	−42	−46	54	352		
	−55	−34	24			186
R parietal lobe (inferior parietal lobule, BA 40)	43	−41	56		369	
	47	−41	55			312
L frontal lobe (middle frontal gyrus, BA 46)	−48	58	9		114	
	−47	57	10			207
R frontal lobe (inferior frontal gyrus, BA 47)	36	26	−2		137	
L cerebellum	−24	−56	−29	245		
	−34	−66	−27		337	
	−49	−63	−27		477	
	−9	−82	−20		2344	
	−26	−76	−26			8089
R cerebellum	18	−83	−33	314		
	17	−48	−32		253	
	31	−51	−31		297	
	18	−81	−28		924	
	43	−61	−27		1953	
	30	−66	−29			7307

Table 2

Mean $iEMG_{burst}$:$iEMG_{pre}$ ratio for each muscle.

Task	First dorsal interosseous	Second dorsal interosseous	Extensor digitorum	Abductor digiti minimi
Easy	5.39±0.48	8.02±0.72[b]	14.70±1.69	7.39±0.84
Hard	6.71±0.54[a]	4.90±0.33	12.09±1.12	6.35±0.50

Values are mean±standard error.

[a]significantly greater than Easy.

[b]significantly greater than Hard.