Task dependency of motor adaptations to an acute noxious stimulation

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Hug F, Hodges PW, Tucker K. Task dependency of motor adaptations to an acute noxious stimulation. J Neurophysiol 111: 2298–2306, 2014. First published March 19, 2014; doi:10.1152/jn.00911.2013.—This study explored motor adaptations in response to an acute noxious stimulation during three tasks that differed in the number of available degrees of freedom. Fifteen participants performed three isometric force-matched tasks (single leg knee extension, single leg squat, and bilateral leg squat) in three conditions (Control, Pain, and Washout). Pain was induced by injection of hypertonic saline into the vastus medialis muscle (VM; left leg). Supersonic shear imaging was used to measure muscle shear elastic modulus as this is considered to be an index of muscle stress. Surface electromyography (EMG) was recorded bilaterally from six muscles to assess changes in neural strategies. During tasks with fewer degrees of freedom (knee extension and single leg squat task), there was no change in VM EMG amplitude or VM shear elastic modulus. In contrast, during the bilateral leg squat, VM (−32.9 ± 15.8%; P < 0.001) and vastus lateralis (−28.7 ± 14.8%; P < 0.001) EMG amplitude decreased during Pain. This decrease in activation was associated with reduced VM shear elastic modulus (−17.6 ± 23.3%; P = 0.029) and reduced force produced by the painful leg (−10.0 ± 10.2%; P = 0.046). This work provides evidence that when an obvious solution is available to decrease stress on painful tissue, this option is selected. It confirms the fundamental assumption that motor adaptations to pain aim to alter load on painful tissue to protect for further pain and/or injury. The lack of adaptation observed during force-matched tasks with fewer degrees of freedom might be explained by the limited potential to redistribute stress or a high cost induced by such a compensation.

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motor adaptation is to reduce load within the painful region. However, the relationship between myoelectrical activity and muscle stress is not straightforward, even during isometric contractions. This is because of limitations inherent to the electromyographic (EMG) technique (Farina et al. 2004b; Hug 2011) and because muscle stress is the combination of both active and passive stress. For example, it is possible that the neural drive to the muscle is not modified during a task but the load within the muscle is altered by small changes of limb/joint positions. This is because these small changes in position (that cannot be completely avoided, even during an isometric task) can alter passive stress. In other words, the goal of changing load on the painful muscle tissue could be achieved by altering muscle recruitment (quantified by EMG) and/or by altering the passive stress (or force).

Muscle shear elastic modulus measured by a shear wave elastographic technique [supersonic shear imaging (SSI)] is linearly related to muscle stress (Bouillard et al. 2011, 2012; Yoshitake et al. 2013). Therefore, SSI can quantify relative changes in muscle stress during isometric contractions (Bouillard et al. 2012, 2014). Taking advantage of this experimental technique, Tucker et al. (2014) reported no systematic reduction in stress within the painful muscle during an isometric force-matched knee extension. This absence of systematic unloading of the painful region might reflect a limited potential to alter load sharing between muscles while maintaining force output during this simple isometric task. This concurs with the observation that, when the force production capacity of one agonist muscle is reduced (through fatigue or simulated paralysis), participants increase the recruitment of all agonists, instead of recruiting only the effective muscles (de Rugy et al. 2012). Alternatively, it is possible that this absence of consistent change in muscle stress (Tucker et al. 2014) might be explained by the characteristics of the studied muscle [vastus lateralis (VL)]. Considering the unique role of the vastus medialis (VM; particularly its distal part, VMO) as the only muscle of the quadriceps group with the potential to control lateral motion of the patella (Goh et al. 1995) and the more consistent changes observed in VM than VL during clinical knee pain (e.g., delayed onset of activity of VM during stepping; Cowan et al. 2001), it is possible that changes in muscle stress are more likely to be observed in VM than VL during local muscle pain. It is also possible that the force level used in our previous study [i.e., 10% of maximal voluntary contraction (MVC); Tucker et al. 2014] was insufficient to trigger a reduction in stress in VL. This is because more consistent changes in myoelectrical activity are often observed at higher force levels (Bank et al. 2013).
Here we investigated the effect of saline-induced acute muscle pain on motor adaptations during tasks with differing degrees of freedom (i.e., the number of muscles and joints involved in force production). SSI was used to quantify changes in stress within the painful muscle (VM), and myoelectric activity was recorded from multiple muscles to assess changes in neural control strategies. We compared three isometric force-matched tasks with increasing degrees of freedom, i.e., single leg knee extension (20% of MVC), single leg squat, and bilateral leg squat. We hypothesized that both myoelectric activity and stress would reduce in the painful muscle (VM) during the multijoint tasks (single and bilateral leg squat). This reduced muscle activity and stress would be compensated by increased activity of hip extensor muscles (single leg squat) or increased force produced by the contralateral leg (bilateral leg squat). However, a decrease in stress will not be systematically observed in VM during the single-joint task (knee extension), where fewer options are available for compensation for a reduced force contribution from VM.

MATERIALS AND METHODS

Participants. Fifteen healthy volunteers, with no history of lower limb pain that had limited function or for which they had sought treatment, participated in this experiment (age: 24 ± 5 yr; weight: 66 ± 12 kg; height: 168 ± 7 cm; 5 females). Participants were informed of the methods used before providing written consent. The Institutional Medical Research Ethics Committee (University of Queensland) approved the study, and all the procedures conformed to the Declaration of Helsinki.

Experimental set up. Participants performed three experimental isometric tasks, i.e., knee extension (left leg), single leg squat (left leg), and bilateral leg squat. For the isometric knee extension, participants sat on a plinth with their back and upper legs supported (Fig. 1A), the torso reclined by 10° from upright, and the arms crossed over their chest. A strap around the pelvis minimized changes in body position throughout the experiment. Isometric knee extension force was measured with a force transducer (30 lb, LSB300; Futek) attached via a strap around the test leg just above the ankle. For both single and bilateral leg squat, the participants stood on force plates (model 9260AA6; Kistler). Foot position was marked on the force plate at the beginning of the experiment. For the single leg squat, the participant’s left foot was positioned on the left force plate and the right leg was held away from the right force plate in a similar position between conditions. For the bilateral leg squat the feet were positioned on separated force plates. The knee angle was matched at ~55° from full extension for all tasks. Two horizontal bars (set at 80% of the participant’s height) pressed against the participant’s shoulders and resisted cephalad body movement during the isometric squats (Fig. 1, B and C). For the squattting tasks, the participant’s shoulders and ankles were aligned before testing began.

Force data. Isometric knee extension force was measured by a force transducer. For single and bilateral leg squat, force was measured using force plates. For the bilateral leg squat, the force provided as feedback was the sum of the left and right Fz (i.e., vertical force). All force data were sampled at 1 kHz (Power1401 Data Acquisition System; Cambridge Electronic Design) and low-pass filtered (20 Hz, 4th order Butterworth filter) offline.

Surface EMG. Myoelectrical activity was recorded bilaterally with surface EMG electrodes from six muscles (i.e., total of 12 muscles): soleus (SOL), VM, VL, biceps femoris-long head (BF), gluteus maximus (GM), and erector spinae at L4 level (ES). These muscles were chosen because they can directly or indirectly contribute to the production of force during the studied tasks. For each muscle, a pair of self-adhesive Ag/AgCl electrodes (Blue sensor N; Ambu) was attached to the skin with an inter-electrode distance of 20 mm (center-to-center). Before electrode application, the skin was cleaned with abrasive gel (Nuprep; D.O. Weaver & Co.) and alcohol. The ground electrode (half a Universal Electrosurgical Pad, 3M Health Care) was placed on the skin over the tibia of the right leg. EMG data were preamplified 1,000 times, band-pass filtered (20–500 Hz) online (Neurolog; Digitimer), and sampled at 1 kHz using a Power1401 Data Acquisition System with Spike2 software (Cambridge Electronic Design).

Shear elastic modulus. An Aixplorer ultrasound scanner (version 6.0; Supersonic Imagine, Aix-en-Provence, France), coupled with a linear transducer array (4–15 MHz, SuperLinear 15–4; Veronica, Tours, France), was used in SSI mode (musculoskeletal preset). Assuming a linear elastic behavior (Bercoff et al. 2004), the muscle shear elastic modulus (µ) was calculated as follows:

\[ \mu = \rho V_s^2 \]  \hspace{1cm} (1)

where \( \rho \) is the muscle mass density (1,000 kg/m³) and \( V_s \) is the shear wave speed. Maps of the shear elastic modulus were obtained at one sample per second (Fig. 2).

The ultrasound transducer was placed on the distal portion of the VM muscle belly, respecting the muscle fiber direction when possible. As described elsewhere (Bouillard et al. 2012, 2013), the optimal transducer location was determined using a B-mode ultrasound image as a region with a muscle thickness of at least 1 cm that avoided hypoechoic regions that relate to fascia and tendon tissue. This

Fig. 1. Experimental setup. Isometric knee extension was performed in three different experimental tasks with increasing degrees of freedom. A: monarticular knee extension with the participant seated on a plinth and isometric knee extension force measured with a force transducer attached via a strap around the test leg. B: single leg squat with the left foot positioned on the left force plate. C: bilateral leg squat with each foot positioned on a separated force plate. Two horizontal bars (set at 80% of the participant’s height) pressed against the participants’ shoulders and resisted cranial body movement during the squats.
ADAPTATIONS TO PAIN ARE TASK DEPENDENT

The transducer location remained constant between tasks and conditions. Location was marked on the skin using a waterproof marker so that the transducer was superposed onto the B-mode image, with the color scale depicting gradient of shear elastic modulus (scale in kPa at bottom right). To obtain a representative value, the shear elastic modulus (in kPa) was averaged over the region indicated by the white rectangle. In this example the shear elastic modulus was decreased from 38 to 12 kPa from Control to Pain. Note that the data for each condition were averaged over 8 consecutive maps in 3 separate contractions (i.e., 24 maps).

Experimental tasks. The three experimental tasks (i.e., knee extension, single and bilateral leg squat) were performed in a randomized order. For the isometric knee extension, before commencement of the experimental trial, three maximal isometric voluntary contractions were performed for 3 s, separated by at least 90 s for recovery. The maximum force was considered the best performance (MVC). The experimental trial, three maximal isometric voluntary contractions (i.e., Control, Pain, and Washout) were performed for 3 s, separated by at least 90 s for recovery. The maximum force was considered the best performance (MVC). The mean square EMG amplitude was quantified over the same 8-s period. As the electrode location did not change throughout the experiment, muscle activity was compared between conditions (i.e., Control, Pain, and Washout) and between tasks (i.e., single leg isometric knee extension and single and bilateral leg squat) without normalization.

Statistical analysis. One participant was unable to maintain balance during the single leg squat, and therefore 14 participants are included for this task. Statistics were performed using Statistica (Statsoft). Data were transformed if distributions did not pass the Shapiro-Wilk normality test (only observed for some EMG data). When the log transformation was not satisfactory, an inverse transformation was performed (only for GM for single leg squat and ES for both knee extension and single leg squat). Pain intensity was compared between conditions (knee extension and single and bilateral leg squat) and Muscle state (during contraction and at rest) using a repeated-measures ANOVA. To verify that force was matched between conditions, recorded force was compared among Conditions (Control, Pain, and Washout) using a repeated measures ANOVA (for each task separately).

Assess putative between-leg compensation during bilateral squats, participants were aware that the target torque was provided by summation of force produced by both legs but were not instructed regarding any load sharing strategy to produce force.

During the testing period, participants performed three short (15 s) constant force isometric contractions with 60 s of rest between each contraction. Participants increased the force to the target over ~2 s, held this force as steady as possible for 15 s, and then returned to rest. This was repeated in three experimental conditions: Control, Pain, and Washout for each experimental task (knee extension, single, and bilateral leg squat). An experimenter carefully checked that force was well maintained. If not, the participants were instructed to make a correction. Participants rested by sitting between each contraction but did not change their foot placement between contractions within a condition or between conditions. Foot placement was optimized separately for the single and bilateral squat task.

Experimental pain. For each of the three Pain conditions (i.e., one for each of the experimental tasks) pain was induced by injection of hypertonic saline (0.5-ml bolus 6.7% NaCl) in the VM of the left leg. Saline was injected using a 25 G × 25 mm hypodermic needle at ~5 cm proximal to the patella, close to the ultrasound transducer location. Participants rated pain intensity on an 11-point numerical rating scale, anchored with “no pain” at 0 and “maximum imaginable pain” at 10. Test contractions began after pain was reported to be ≥2/10. Following each contraction, participants rated pain intensity experienced during the task and during the rest period. Participants recorded the area of pain on a standardized diagram of the thigh after completion of each pain condition. The Washout condition (which followed each Pain condition) was initiated >3 min after pain had completely resolved.

For each force-matched contraction, an 8-s period at the middle of the force plateau was used for analysis. For the squat tasks, the average amplitude of force was measured in the vertical axis (i.e., \(F_z\), \(F_z\) for the left and right leg, respectively).

The root mean square EMG amplitude was quantified over the same 8-s period. As the electrode location did not change throughout the experiment, muscle activity was compared between conditions (i.e., Control, Pain, and Washout) and between tasks (i.e., single leg isometric knee extension and single and bilateral leg squat) without normalization.

The data were processed using Matlab (The Mathworks, Natick, MA). From each force-matched contraction, an 8-s period at the middle of the force plateau was used for analysis. For the squat tasks, the average amplitude of force was measured in the vertical axis (i.e., \(F_z\), \(F_z\) for the left and right leg, respectively).

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and Conditions (Control, Pain, and Washout) using a repeated-measures ANOVA.

To consider if the stress within the VM was similar during the Control contractions of each task, VM shear elastic modulus measured during the Control condition was first compared between the three tasks using a repeated-measures ANOVA. Then, for each task separately, shear elastic modulus measured in VM was compared between Conditions (Control, Pain, and Washout) using a repeated-measures ANOVA. EMG amplitude for each muscle and each task (separately) was compared between Conditions (Control, Pain, and Washout) using repeated-measures ANOVAs. To compare the effect of pain on muscle stress and muscle activity between the three tasks, the changes in shear elastic modulus and in myoelectric activity measured in VM (painful region) between the Control and Pain contractions, and the Control and Washout contractions (expressed as %Control), were compared between the Tasks (knee extension and single and bilateral leg squat) using a repeated-measures ANOVA. To determine whether the changes in VM shear elastic modulus were linearly related to the changes in VM EMG amplitude, a model II regression was performed (reduced major axis, “Isfitgmm” function in Matlab). The same regression analysis was performed between the changes in VM and VL EMG amplitude. All data are reported as mean ± SD unless stated otherwise. For each ANOVA, partial eta-squared ($\eta^2$) was calculated as measures of effect size. For the other ANOVAs, values of 0.01, 0.06, and >0.14 were considered as small, medium, and large, respectively. Post hoc analyses were performed using the Tukey test. $P$ values <0.05 were considered significant.

We performed additional data analysis to evaluate individual changes in EMG amplitude during the bilateral leg squat with Pain for each muscle of the nonpainful leg. A muscle was considered to have increased or decreased activity if the change was >15% of Control (Hodges et al. 2013). Data are presented descriptively for this analysis.

RESULTS

Pain. Pain was localized around the site of the saline injection (Fig. 3) except in one participant who reported an additional area of referred pain in the anterior knee region following each saline injection. The average reported pain intensity during the contraction was 5.3 ± 1.4, 4.8 ± 1.2, and 5.0 ± 1.4 for knee extension and single and bilateral leg squat, respectively. At rest (after contraction), pain intensity was 5.8 ± 1.0, 5.0 ± 1.1, and 5.2 ± 1.2 for knee extension and single and bilateral leg squat, respectively. Pain intensity was not different between the three tasks (main effect Task: $P = 0.12; \, \eta^2 = 0.14$) and did not differ between states with the muscle contracted or relaxed (main effect Muscle state: $P = 0.27; \, \eta^2 = 0.09$).

Force data. The produced force was 80 ± 20 N (i.e., 19.7 ± 0.6% of MVC), 800 ± 151 N, and 939 ± 141 N for knee extension and single and bilateral leg squat, respectively. Note that the body weight of participants (66 ± 12 kg) was used to calculate the target force of the squat tasks. Although, participants matched the force target accurately between Conditions (Control, Pain, and Washout) during knee extension ($P = 0.31; \, \eta^2 = 0.08$) and single leg squat ($P = 0.81; \, \eta^2 = 0.02$), a significant effect of Condition ($P = 0.046; \, \eta^2 = 0.19$) was found for bilateral leg squat. For this task, higher force (i.e., sum of $F_L$ and $F_R$) was produced during Pain (942 ± 142 N) than during Control (939 ± 141 N; $P = 0.036$) trials. Although significant, the increase in force was small (~3 N; i.e., 0.3% of the force produced during Control) and was explained by an increase in force produced by the nonpainful leg (see below). No other differences were found (Control vs. Washout: $P = 0.44$; Pain vs. Washout: $P = 0.30$).

During the bilateral leg squat, a significant effect of Leg ($P = 0.020; \, \eta^2 = 0.32$), Condition ($P = 0.045; \, \eta^2 = 0.20$), and a significant Condition × Leg interaction ($P = 0.0002; \, \eta^2 = 0.45$) was found for $F_L$. The force produced under the painful leg ($F_{PL}$) was significantly less than that under the nonpainful leg ($F_{RN}$) during Pain (411 ± 117 vs. 531 ± 61 N; $P = 0.0001$). This contrasts the more evenly distributed force between legs during Control (459 ± 100 vs. 480 ± 65 N for the left and right leg, respectively; $P = 0.76$) and Washout (448 ± 102 vs. 492 ± 63 N for the left and right leg, respectively; $P = 0.07$) conditions. Compared with Control, $F_{PL}$ (force under the painful leg) was less during Pain (−10.0 ± 10.2%; $P = 0.046$) whereas $F_{RN}$ (force under the nonpainful leg) increased (+11.5 ± 11%; $P = 0.026$; Fig. 4). The uneven distribution of force between legs during Pain recovered after pain resolved with no difference between force distributed to either leg in the Control and Washout conditions: $F_{PL}$ ($P = 0.98$) and $F_{RN}$ ($P = 0.96$).

Surface EMG. During knee extension, there was no main effect of Condition on EMG amplitude of SOL ($P = 0.073; \, \eta^2 = 0.17$), VM ($P = 0.20; \, \eta^2 = 0.11$), VL ($P = 0.86; \, \eta^2 = 0.01$), or BF ($P = 0.27; \, \eta^2 = 0.09$). However, a
significant effect of Condition was found for EMG of both GM ($P = 0.02$; $\eta^2 = 0.20$) and ES ($P = 0.004$; $\eta^2 = 0.32$). GM (+38.1 ± 61.0%; $P = 0.022$) and ES (+57.4 ± 65.3%; $P < 0.001$) EMG amplitude was significantly higher during Pain than Control (Fig. 5). The amplitude of GM ($P = 0.85$) and ES ($P = 0.62$) EMG were similar during the Washout and Control contractions.

No main effect of Condition was found during single leg squat for BF ($P = 0.27$; $\eta^2 = 0.09$) or ES ($P = 0.24$; $\eta^2 = 0.11$). In contrast, there was a significant main effect of Condition for SOL ($P = 0.0025$; $\eta^2 = 0.37$), VM ($P = 0.0043$; $\eta^2 = 0.34$), VL ($P = 0.003$; $\eta^2 = 0.36$), and GM ($P = 0.013$). EMG activity was higher during Pain compared with Control for SOL (+23.2 ± 33.9%; $P = 0.004$) and GM (+11.5 ± 10.5%; $P = 0.003$; $\eta^2 = 0.43$). EMG was also higher during Washout than Control for SOL (+22.8 ± 23.7%; $P = 0.011$), VL (+8.9 ± 10.5%; $P = 0.016$), and GM (+14.5 ± 14.8%; $P = 0.02$) and than Pain for VM (+15.1 ± 19.3%; $P = 0.003$) and VL (+11.6 ± 11.9%; $P = 0.005$).

For bilateral leg squat, EMG data for the painful (left) and nonpainful (right) legs were analyzed separately. For the painful leg, there was no significant main effect of Condition for SOL ($P = 0.16$; $\eta^2 = 0.12$), BF ($P = 0.29$; $\eta^2 = 0.08$), GM ($P = 0.21$; $\eta^2 = 0.10$), and ES ($P = 0.72$; $\eta^2 = 0.02$). In contrast, VM ($P < 0.0001$; $\eta^2 = 0.66$) and VL ($P < 0.0001$; $\eta^2 = 0.67$) differed between Conditions; EMG amplitude was lower during Pain than Control (−32.9 ± 15.8% and −28.7 ± 14.8% for VM and VL, respectively; $P < 0.001$) and Washout (−27.6 ± 16.9% and −24.0 ± 15.2% for VM and VL, respectively; $P < 0.001$). There was no difference between Control and Washout (VM: $P = 0.589$, VL: $P = 0.515$). For the nonpainful leg, there was a significant effect of Condition only for BF ($P = 0.047$; $\eta^2 = 0.19$), but post hoc analysis did not identify any significant difference ($P > 0.07$). No other significant main effect was found ($P$ values ranged from 0.07 to 0.62; 0.03 < $\eta^2 < 0.12$). Table 1 provides a visual summary of the changes in EMG amplitude observed for each muscle and each participant in the nonpainful leg. This analysis reveals that participants used different motor strategies [e.g., increased knee extension (VM and VL)] for participants 1, 7, 8, and 15 and increased hip extension (GM and/or BF) for participants 2, 3, 7, 9, 13 and 15] to compensate for the decrease in force produced by the painful leg.

For each task a strong linear relationship was found between the change in VM and VL EMG amplitudes measured during Pain and expressed in percentage of Control (R² = 0.81, 0.60, and 0.94 for knee extension, single leg squat, and bilateral leg squat, respectively).

Finally, to determine if the change in VM EMG amplitude was similar among tasks, the percentage of change in VM EMG amplitude (from Control) determined for both Pain and Washout was compared between the tasks. The percentage change in VM EMG was influenced by Task ($P < 0.0001$; $\eta^2 = 0.54$). For each muscle and each participant, EMG amplitude (% control) was changed by $15\%$ of Control values. Otherwise, the EMG amplitude was considered unchanged. This analysis reveals that each participant used a different motor strategies to reach the same mechanical outcome (increased force produced by the nonpainful leg). SOL, soleus; VM, vastus medialis; VL, vastus lateralis; BF, biceps femoris; GM, gluteus maximus; ES, erector spinae.

**Table 1.** Individual changes in EMG amplitude (% control) of the nonpainful leg during bilateral leg squat

<table>
<thead>
<tr>
<th>Participant</th>
<th>SOL</th>
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<th>VL</th>
<th>BF</th>
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</tbody>
</table>

For bilateral leg squat, EMG data for the painful (left) and nonpainful (right) legs were analyzed separately. For the painful leg, there was no significant main effect of Condition for SOL ($P = 0.16$; $\eta^2 = 0.12$), BF ($P = 0.29$; $\eta^2 = 0.08$), GM ($P = 0.21$; $\eta^2 = 0.10$), and ES ($P = 0.72$; $\eta^2 = 0.02$). In contrast, VM ($P < 0.0001$; $\eta^2 = 0.66$) and VL ($P < 0.0001$; $\eta^2 = 0.67$) differed between Conditions; EMG amplitude was lower during Pain than Control (−32.9 ± 15.8% and −28.7 ± 14.8% for VM and VL, respectively; $P < 0.001$) and Washout (−27.6 ± 16.9% and −24.0 ± 15.2% for VM and VL, respectively; $P < 0.001$). There was no difference between Control and Washout (VM: $P = 0.589$, VL: $P = 0.515$). For the nonpainful leg, there was a significant effect of Condition only for BF ($P = 0.047$; $\eta^2 = 0.19$), but post hoc analysis did not identify any significant difference ($P > 0.07$). No other significant main effect was found ($P$ values ranged from 0.07 to 0.62; 0.03 < $\eta^2 < 0.12$). Table 1 provides a visual summary of the changes in EMG amplitude observed for each muscle and each participant in the nonpainful leg. This analysis reveals that participants used different motor strategies [e.g., increased knee extension (VM and VL)] for participants 1, 7, 8, and 15 and increased hip extension (GM and/or BF) for participants 2, 3, 7, 9, 13 and 15] to compensate for the decrease in force produced by the painful leg.

For each task a strong linear relationship was found between the change in VM and VL EMG amplitudes measured during Pain and expressed in percentage of Control (R² = 0.81, 0.60, and 0.94 for knee extension, single leg squat, and bilateral leg squat, respectively).

Finally, to determine if the change in VM EMG amplitude was similar among tasks, the percentage of change in VM EMG amplitude (from Control) determined for both Pain and Washout was compared between the tasks. The percentage change in VM EMG was influenced by Task ($P < 0.0001$; $\eta^2 = 0.54$). For each muscle and each participant, EMG amplitude (% control) was changed by $15\%$ of Control values. Otherwise, the EMG amplitude was considered unchanged. This analysis reveals that each participant used a different motor strategies to reach the same mechanical outcome (increased force produced by the nonpainful leg). SOL, soleus; VM, vastus medialis; VL, vastus lateralis; BF, biceps femoris; GM, gluteus maximus; ES, erector spinae.
0.59), Condition (Pain and Washout; $P < 0.0001$; $\eta^2 = 0.73$), and there was a significant Task $\times$ Condition interaction ($P < 0.0001$; $\eta^2 = 0.59$). Pain was associated with a larger decrease in VM activity during bilateral leg squat ($-32.9 \pm 15.8\%$) than single leg squat ($-6.5 \pm 11.4\%; P = 0.0001$) and knee extension ($-5.3 \pm 14.9\%; P = 0.0001$). There was no difference in percentage change of VM EMG between knee extension and single leg squat ($P = 0.99$). Percentage change of VM activity during Washout did not differ between tasks (all $P$ values $> 0.99$).

SS1. A main effect of Task ($P < 0.0001$) was found for shear elastic modulus measured during the Control condition. Modulus was higher during single leg squat (76.6 ± 30.5 kPa) than both knee extension (44.7 ± 20.1 kPa; $P = 0.0003$) and bilateral leg squat (57.4 ± 23.9 kPa; $P = 0.008$). No difference was found between knee extension and bilateral leg squat ($P = 0.10$).

Although there was no main effect of Condition for shear elastic modulus during knee extension ($P = 0.22$; $\eta^2 = 0.10$) or single leg squat ($P = 0.24$; $\eta^2 = 0.10$), the effect of Condition was significant for bilateral leg squat ($P = 0.025$; $\eta^2 = 0.24$) (Fig. 6). In that task, shear elastic modulus of VM was lower during Pain than Control (48.2 ± 22.7 vs. 57.9 ± 23.2 kPa; $P = 0.029$). There was no difference between Pain and Washout (56.1 ± 24.4 kPa; $P = 0.09$) or between Control and Washout ($P = 0.87$).

Finally, to determine if the change in shear elastic modulus was similar between tasks, the percentage change in VM shear elastic modulus (relative to Control) determined for both Pain and Washout was compared between tasks. Although there was no main effect of Task ($P = 0.53$; $\eta^2 = 0.05$), the main effect of Condition (Pain and Washout; $P = 0.03$; $\eta^2 = 0.32$) and interaction between Task $\times$ Condition ($P = 0.011$; $\eta^2 = 0.29$) were significant. Pain induced a significantly greater decrease in VM shear elastic modulus during bilateral leg squat ($-17.6 \pm 23.3\%$) than single leg squat ($-4.9 \pm 14.2\%; P = 0.016$). Bilateral leg squat was not different to unilateral knee extension ($-7.1 \pm 14.5\%; P = 0.10$).

Relationship between the changes in shear elastic modulus and EMG. Although we found a strong linear relationship between the changes in VM EMG amplitude and the changes in shear elastic modulus during the Pain condition (expressed as percentage of Control) for bilateral leg squat ($R^2 = 0.60$; Fig. 7), no linear relationship was found for knee extension ($R^2 = 0.005$) and single leg squat ($R^2 = 0.17$).

DISCUSSION

This study explored the motor adaptations (in terms of changes in force production, muscle activation and muscle stress) to an acute noxious stimulation during three tasks that differed in their degrees of freedom (i.e., the number of muscles and joints that may be used to perform the task). During tasks with fewer degrees of freedom, i.e., the knee extension and the single leg squat task, the activity of muscles proximal or distal to the painful region increased during pain, but without any change in VM (the painful muscle). In contrast, during the bilateral leg squat, VM and VL muscle activity reduced when pain was induced in VM. This reduction in muscle activity was associated with reduced stress within VM and reduced force produced by the painful leg, and was compensated by an increase in force produced by the nonpainful leg. This work provides strong evidence that when the central nervous system (CNS) is presented with an obvious solution to decrease stress on painful tissue (i.e., another limb can assist in the task), this option is selected. There are two plausible hypotheses to explain the absence of a consistent decrease in muscle stress and EMG amplitude in VM during knee extension and single leg squat. First, there may be limited potential to redistribute stress while maintaining the force output in these tasks with limited degrees of freedom. Second, compensation may be possible, but avoided because of consequences such as a high cost or suboptimal tissue/joint loading induced by such a compensation strategy.

Methodological considerations. It is important to note that the shear elastic modulus values cannot be considered as a
direct estimation of muscle force (in N) but rather an accurate and reliable quantification of changes in muscle force (or stress) as demonstrated both in vivo (Bouillard et al. 2011, 2012; Yoshitake et al. 2013) and in vitro (Koo et al. 2013). We have previously demonstrated that the injection of nonpainful saline (isotonic saline) does not alter the shear elastic modulus measured at rest or during contraction (Tucker et al. 2014). This demonstrates that the relationship between muscle stress and shear elastic modulus is not altered by the injection of saline allowing us to interpret the changes in shear elastic modulus as a change in muscle stress and not tissue hydration.

Care was taken to match, as closely as possible, the stress within the VM during the control conditions between the three experimental tasks. However, the shear elastic modulus was higher (20–30 kPa) during single leg squat than during both knee extension and bilateral squat tasks (no difference between bilateral leg squat and knee extension). As shown in Fig. 6, higher values were mainly observed in one-third of the participants, and these participants were all of greater body mass. To overcome the possibility that this difference in shear elastic modulus between tasks would influence, the results we performed analysis on each task separately and compared data between tasks as percentage change from the Control condition.

Finally, although adaptations have been reported immediately after the induction of acute experimental pain [e.g., motor unit activation (Tucker and Hodges 2009) and timing of muscle activity during dynamic tasks (Hodges et al. 2009)], it is important to consider that motor adaptation may require greater repetitions or trial and error. In our study, participants performed three short (15 s) constant force isometric contractions with 60 s of rest between each contraction. This number of repetitions was sufficient to trigger a systematic adaptation during the bilateral leg squat, where the adaptation strategy is more obvious. However, it may have not been sufficient to trigger adaptation during the knee extension and single leg squat task. Further investigation is required to determine whether consistent change in load are observed during tasks with fewer degrees of freedom with repeated/persistent pain exposure.

**Task dependency of motor adaptations.** Motor adaptations to experimental pain have been hypothesized to reduce load within the painful region to protect from further pain and/or injury (Hodges and Tucker 2011). However, experimental pain studies reporting changes in muscle activity (Bank et al. 2013) or muscle shear elastic modulus (Tucker et al. 2014) during simple isometric force-matched tasks do not provide direct evidence of this proposed mechanical adaptation. Few studies have investigated compensation between limbs during unilateral pain. A redistribution of the force between the legs has been reported during an isometric bilateral plantarflexion where the soleus was the main contributor of the task (i.e., knee angle = 90°) and thus when the only option to unload the painful muscle (soleus) was to increase the force produced by the nonpainful leg (Hug et al. 2014). However, during quiet stance with unilateral pain in VM, no shift in body weight to the nonpainful side was reported (Hirata et al. 2010). The present study shows that when the CNS is presented with an obvious solution to decrease stress on painful muscle (i.e., bilateral compensation during double leg squat), this option is selected and achieved (decrease in VM shear elastic modulus: \(-17.6 \pm 23.3\%\)), consistent with a decreased activation of the painful muscle. It is less clear how the compensation (increase in force) with the nonpainful leg was achieved as no significant difference in EMG amplitude was found. However, the measured force is dependent on both the weight distribution and the force produced by each leg that could be both achieved by different muscle coordination strategies. Consequently, this lack of difference does not mean that no change in EMG activity occurred; rather, it is possible that changes in EMG (when they did occur) differed between participants. For example, Hodges et al. (2013) showed that the same mechanical outcome (spinal stability) is achieved by patterns of muscle activity that differed between participants during acute experimental low back pain. Similarly, individual changes observed in the present study (Table 1) clearly show that participants used different motor strategies to achieve the same mechanical outcome (increased vertical force under the nonpainful leg).

In addition to the reduction of shear elastic modulus and EMG recorded from VM, its synergist VL (a nonpainful muscle of the painful leg) exhibited a similar decrease in EMG amplitude during bilateral leg squat (Fig. 5). As further illustrated by the strong linear relationship found between the change in VM and VL EMG amplitude (\(R^2 = 0.94\)) during
bilateral leg squat, this shows that the CNS simply decreased the recruitment of both agonist muscles instead of selectively reducing activation of the painful muscle alone. The absence of selective adaptation of the painful muscle could be explained by the fact that modification of the common drive between VL and VM (Beck et al. 2012; Mellor and Hodges 2005b) may increase the cost of the control of movement (e.g., higher cost for CNS as a result of an increased number of degrees of freedom to control). It is also possible that the CNS cannot differentiate the descending drive to VM and VL as previously suggested in healthy participants (Place et al. 2006). Interestingly, reduced common drive to the vastii muscle has been shown in people with chronic anterior knee pain (Mellor and Hodges 2005a) suggesting that chronic exposure to pain might trigger such adaptations. Alternatively, it is possible that the reduction in both VL and VM is desirable (and thus purposeful) to ensure the direction of the produced force vector is appropriate for the task and to facilitate unloading of the painful tissue.

An inability (or at least a nonpreference) for the CNS to dissociate the activity of synergist muscles could further explain the lack of a systematic reduction of shear elastic modulus and VM EMG activity in the knee extension task (and to a lesser extent in the single leg squat), where an increase in VL or other synergistic knee extensor muscles would be required to maintain the task. Therefore, we conclude that a systematic and effective redistribution of load sharing between agonist muscles, aimed at decreasing the stress within the painful region, is unlikely to occur during an isometric single joint task where the force is maintained constant, confirming previous SSI (Tucker et al. 2014) and EMG results (Farina et al. 2004a; Hodges et al. 2008). It is important to consider that it remains possible that the change in motor unit discharge observed during acute pain, including the change in the population of motor units recruited to perform the single joint force-matched tasks (Hug et al. 2013; Minami et al. 2012; Tucker et al. 2009), may relate to an attempt to unload the painful part, but that this does not achieve a generalized unloading.

Compensation between hip and knee joints has been reported during dynamic tasks in healthy individuals (e.g., pedaling; Sanderson and Black 2003) and those after anterior cruciate ligament reconstructive surgery (Osternig et al. 2000). Contrary to our hypothesis, and despite increased GM and SOL activity, pain was not associated with decrease VM EMG or stress during the single leg squat. It is important to note that previous studies (Osternig et al. 2000; Sanderson and Black 2003) focused on dynamic activities that could offer additional possibilities of compensation. Future work should extend the present findings to more dynamic, real-life tasks as advances in the SSI technology permit.

Pain model. Hypertonic saline injection is widely used to replicate the nociceptive component of musculoskeletal pain (for review, see Bank et al. 2013). However, our results suggest that the nociceptive irritation caused by hypertonic saline does not respond in a predictable manner to tissue loading. Two interpretations of these data need to be considered. First, it is possible that nociceptive discharge increases with increased contraction level but that this increase is negated by pain inhibitory mechanisms (endogenous pain inhibitory mechanisms; e.g., Vaegter et al. 2014) and no change in pain intensity is observed. Second, a significant decrease in muscle stress was observed during the bilateral leg squat (Hug et al. 2014) demonstrating that when the nervous system is presented with an obvious solution to decrease stress on irritated tissue, this option is selected, even if there is no direct benefit (in terms of pain intensity). However, this adaptation was not systematically observed during tasks with fewer degrees of freedom, where the cost of reducing stress in the painful part may be associated with greater cost to the nervous system or not possible given the high common drive to the main synergist muscles that are performing the task. We believe that this difference between tasks will contribute to a better understanding of motor adaptations to pain, and may provoke a reconsideration of the interpretation of the existing literature on pain adaptation (particularly when using hypertonic saline).

Conclusion and perspectives. Considering the redundancy of the musculoskeletal system, it would be theoretically possible to alter load sharing within a muscle group or between joints while force output is maintained, e.g., decreased force produced by the painful muscle compensated by an increased force for the others. However, this was not observed in the current study during tasks with limited degrees of freedom; the single leg squat or the isometric knee extension tasks. Taken together with the observation that decreased VM EMG during double leg squat was accompanied by a similar decrease in VL EMG, these data suggest that changes in load sharing strategy between these two muscles are neurally constrained, which will likely limit the possibilities of compensation and/or increasing the cost of these compensation such that this option is not systematically selected by the CNS. Because rectus femoris is controlled more independently than the vastii (Place et al. 2006), it is more likely that pain in this muscle would be associated with more systematic changes in stress. This putative muscle-dependency of pain adaptations requires further investigation.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS


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