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Tracking the acquisition of anticipatory postural adjustments during a bimanual load-lifting task: A MEG study

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► To cite this version:

Franck Di Rienzo, Fanny Barlaam, Sébastien Daligault, Claude Delpuech, Alice C Roy, et al.. Tracking the acquisition of anticipatory postural adjustments during a bimanual load-lifting task: A MEG study. Human Brain Mapping, 2019, 40 (10), pp.2955-2966. 10.1002/hbm.24571 . hal-02379153

HAL Id: hal-02379153

<https://hal.science/hal-02379153v1>

Submitted on 12 Dec 2019

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3 **Tracking the acquisition of anticipatory postural adjustments during a bimanual load-**
4 **lifting task: A MEG study**
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8 **Running title:** Acquisition of anticipatory postural adjustments
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Abstract

During bimanual coordination, i.e., manipulating with the dominant hand an object held by the postural hand, anticipatory postural adjustments are required to cancel the perturbations and ensure postural stabilization. Using magnetoencephalography (MEG), we investigated changes mediating the acquisition of anticipatory postural adjustments during a bimanual load-lifting task. Participants lifted a load with their right hand, hence triggering the fall of a second load fixed to their left (postural) forearm. During ACQUISITION, the onset of load-lifting and the fall of the second load were experimentally delayed after few trials. During CONTROL, load-lifting triggered the fall of the second load without delay. Upward elbow rotation decreased with trial repetition during ACQUISITION, hence attesting the ongoing acquisition of anticipatory postural adjustments. Bilateral event-related desynchronisation (ERD) of the alpha rhythm (8-12 Hz) was recorded. Generators of the mu rhythm were found within central and associative motor regions. Their spatial distribution within the hemisphere contralateral to the load-lifting arm was less refined and circumscribed during ACQUISITION compared to CONTROL. Regression analyses emphasized the specific involvement of the precuneus in the right hemisphere contralateral to the postural forearm, and a medial prefrontal region in the left hemisphere. Analyses of the time course power showed that an increase pre-unloading activation within the precuneus and a decrease in post-unloading inhibition within the medial prefrontal region were associated with the acquisition of anticipatory postural adjustments. The study provides original insights into cortical activations mediating the progressive tuning of anticipatory postural adjustments during the acquisition stage of motor learning.

Keywords: motor control, bimanual coordination, mu sensorimotor rhythm, neural plasticity

Introduction

Motor learning classically refers to long-lasting changes in motor behaviors resulting from experience and/or training practice (Schmidt et al. 2018). Historically, experimental research primarily addressed motor learning through the behavioral evaluation of retention, interference and transfer effects (Adams 1987; Lee 1988; Schmidt et al. 2018). At a neurophysiological level, motor learning is mediated by experience-based neural plasticity (Ungerleider et al. 2002; Doyon and Benali 2005; Dayan and Cohen 2011). In a meta-analysis, Hardwick et al. (2013) emphasized the role of cortico-thalamic reorganizations during motor learning of sequential motor skills, i.e., variants of the sequential response time task. These paradigms classically involve the sequential practice of simple actions corresponding to pre-established motor programs (e.g., finger tapping movements). Evaluations of learning effects primarily focus on quantitative aspects of the motor performance such as the movement duration and error rates. By contrast, motor learning paradigms requiring the build-up of new motor programs (e.g., phase coordination paradigms) appeared to engage to a greater extent subcortical structures such as the basal ganglia and the cerebellum. While the type of motor learning influences the nature of experience-based neural plasticity, premotor and primary motor cortex recruitment mediated both types of motor learning (Hardwick et al. 2013).

Contribution of the primary motor cortex to performance changes resulting from practice has been evidenced in several experiments involving bimanual coordination (Donchin et al. 1998; Ioffe et al. 2003; Kazennikov et al. 2006, 2007, 2008; Rueda-Delgado et al. 2014). The bimanual load-lifting task represents a specific case of bimanual coordination: the lifting hand is involved in the manipulation of the object, whereas the contralateral hand endorses a “*postural*” role (Dufossé et al. 1987). Voluntary actions trigger corollary postural perturbations which are regulated by the central nervous system in order to minimize their disturbing effects on balance (Bouisset and Zattara 1981; Massion 1992 for an overview). One of the function of anticipatory postural adjustments is to minimize the disturbance of the postural orientation of the body segment that serve as a reference frame for the organization of movement (Massion et al., 1999). The bimanual load-lifting task thus requires coordinating the load-lifting hand with the postural control of the forearm supporting the load

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3 (Hugon et al. 1982; Dufossé et al. 1987). At first, load-lifting destabilizes the forearm but, over time,
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5 anticipatory postural adjustments enable to cancel this perturbation. As a result, the upward elbow
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7 rotation decreases with practice. The acquisition of this anticipatory process thus requires the central
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9 integration of postural disturbances, hence resulting in the progressive tuning of a reactive control into
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11 a proactive one (Massion et al. 1999). This anticipatory postural control is progressively set up during
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13 childhood and refined during adolescence (Schmitz et al. 2002; Schmitz and Assaiante 2002; Barlaam
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15 et al. 2012).
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19 The bimanual load-lifting task represents an ecological approach to the study of anticipatory
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21 postural adjustments. Indeed, this posture-movement coordination is frequently experienced in
22
23 everyday life, for instance when washing dishes, opening a can, etc. From its very first experimental
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25 version (Hugon et al. 1982), participants had their postural forearm equipped with a platform
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27 supporting a load, and they were required to voluntarily lift the load with the contralateral hand. Hence,
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29 it has early been referred to as the “waiter’s task” with reference to the waiter’s need to stabilize the
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31 forearm posture of the upper limb supporting the plate while concomitantly manipulating the drink
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33 with the other. This first “voluntary” experimental condition was compared to an “imposed” unloading
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35 condition where the load was lifted by the experimenter while the participant remained passive
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37 (Hugon et al. 1982; Dufossé et al. 1985, 1987). Paulignan et al. (1989), tested whether a variant of the
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39 waiter’s task would elicit learning effects (i.e., improved post-unloading postural stabilization of the
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41 forearm). They designed new experimental conditions where the unloading was triggered by a
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43 movement of the opposite arm occurring in the contralateral space. Learning effects of greater
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45 amplitude were recorded when the voluntary unloading action involved joints and force levels
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47 matching those applied to the forearm supporting the load (i.e., typically lifting the same load by an
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49 elbow-joint flexion), compared to movements involving other joints and weaker force levels (e.g.,
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51 pressing a button with the wrist). In other words, voluntarily lifting a load with the dominant arm by
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53 flexing the elbow, hence triggering the fall of a second load (of identical weight) attached to the non-
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55 dominant arm on the opposite side, represents a relevant experimental adaptation of the waiter task.
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57 This paradigm enables to study the progressive build-up of efficient postural regulations. Importantly,
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3 from a fundamental standpoint, it provides a spatial and functional segregation of motor (load-lifting)
4 and postural (forearm stabilization) control associated with posture-movement coordination. Crucially,
5 this bimanual load-lifting coordination is *artificial*, i.e., it has reduced ecological validity compared to
6 the original bimanual load-lifting coordination. This makes it particularly suitable to the study of the
7 acquisition of new anticipatory postural adjustments.
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14 Past experiments investigated the bimanual load-lifting task from behavioral and peripheral
15 neurophysiological recordings (for a review, see Massion et al. 1999). Reports of central nervous
16 system activities remain sparse with a limited number of functional brain imaging experiments. Using
17 magnetoencephalography (MEG), Ng. et al. investigated the brain networks controlling the pre-lifting
18 phase (Ng et al. 2011, 2013a, b). They underlined the involvement of the premotor, parietal and
19 primary sensorimotor cortices, as well as basal-ganglia and thalamic structures. However, which
20 modifications of the brain activity could reflect the acquisition of anticipatory postural adjustments
21 while learning a new bimanual load-lifting coordination is till unknown. Motor learning paradigms
22 classically investigate brain activity before and after an experimental intervention including a training
23 phase. Classically, motor learning is related to brain activity associated with the retention, resistance to
24 interferences and transfer of performance changes recorded at the behavioral level (Doyon et al. 2002;
25 Seidler 2010; Rémy et al. 2010). Very few studies sought to delineate the brain correlates mediating
26 the acquisition stage of motor learning, i.e., trial-to-trial performance changes occurring at the single-
27 session level. In recent motor learning frameworks, this acquisition stage corresponds to the “fast”
28 learning stage preceding the slow, consolidation, automation and retention stages of motor learning
29 (Doyon et al. 2003, 2011; Doyon and Benali 2005; Luft and Buitrago 2005). The bimanual load-lifting
30 task presents with the advantage of enabling the study of this acquisition stage, while manipulating the
31 possibility to improve postural stabilization on a trial-to-trial basis. Transcranial magnetic stimulation
32 data evidenced the specific contribution of the primary motor cortex to the acquisition of anticipatory
33 postural adjustments (Kazennikov et al. 2006, 2007, 2008). The aim of the present study was to
34 extend, using MEG, current knowledge regarding brain activities mediating the acquisition of
35 anticipatory postural adjustments.
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3 Previous studies that exploited the bimanual load-lifting task in its learning version faced the
4 fact that, in adults without neurological pathologies at least, the performance reaches a plateau quite
5 quickly (Paulignan et al., 1989; Barlaam et al., 2016). A reduced number of trials in which learning
6 processes are at work thus limit the possibility to characterize changes in the brain oscillatory activity
7 recorded with MEG, and represents a methodological challenge to the study of anticipatory postural
8 adjustments acquisition. In a pioneering study, Berrigan and Simoneau (2007) experimentally delayed
9 the consequences of a voluntary movement on the body posture. Participants were attached to a cable
10 supporting a load that tended to pull them backward. The authors compared an experimental condition
11 where the forward destabilization of the body triggered by the voluntary unloading of the cable (using
12 an electronic switch device) occurred immediately (i.e., 0 ms), after long (i.e., 300 ms) or short (i.e.,
13 600 ms) delays. Participants adjusted their balance strategies under the immediate and short delay
14 conditions, hence attesting motor learning, but not after the long delay. In the learning variant of the
15 bimanual load-lifting task, we hypothesized that after the postural stabilization reaches a plateau, by
16 artificially delaying the timing of the fall of the load suspended to the postural forearm following the
17 contralateral load-lifting, we should be able to experimentally increase the length of the acquisition
18 phase. By contrast, when the load-lifting triggers the fall of the load with the shortest possible delay
19 and without changes, the acquisition process would end quickly. Interestingly, in the two conditions
20 the load-lifting movement is the same and it triggers in the two cases an upward rotation of the
21 postural elbow. However, depending on the condition, a regular decrease of the maximal amplitude of
22 this perturbation would sign the presence of an on-going acquisition process, while this maximal
23 amplitude should plateau after few trials once the acquisition phase terminates. We hypothesized that
24 i) manipulating the delay would enable to be in an acquisition state along the repetition of the trials,
25 and this should be revealed by a regular decrease of the elbow upward rotation, ii) the acquisition of
26 new anticipatory postural adjustments would be associated with specific activation patterns within
27 central brain regions, specifically primary sensorimotor structures and that trial-to-trial postural
28 performance variations should enable to track the acquisition process within regions pertaining to this
29 network.

Methods

Participants

Sixteen healthy adults volunteered to participate in the experiment (11 males, 27 ± 3.83 years). All were right-handed according to the Edinburgh Handedness Inventory (Oldfield 1971). Written informed consent was obtained according to the guidelines of the Declaration of Helsinki. The study was approved by the local ethics committee (South East IV Committee for the Protection of Persons).

Experimental settings

Participants seated under the MEG helmet. A wooden table was placed above the right knee where their right arm could lie comfortably (Figure 1A). The left arm was positioned adjacent to the trunk, with the elbow fixed to a mobile support stabilizing a horizontal forearm position, with only one degree of freedom in the sagittal plane (Figure 1B). The participants were instructed to keep their left forearm horizontal in a semi-prone position to ensure a natural and comfortable posture of reference. The participants' left arm was then equipped with a wristband equipped with a vacuuming switch system (30 kN/m^2) able to support an 850 g load. The load was released by means of 3.5 kN/m^2 air pulses (Figure 1B).

*** Insert Figure 1 about here ***

Participants first kept their gaze fixed during 2s on a 10 cm light spotted at the base of the load to avoid eye movements. The load laid on a force plate sensor at 45 % of the maximal arm reach (Figure 1A). The participants were instructed to lift the load with their right hand when the light faded out (Figure 1C), hence triggering the release of the load on the left forearm (Figure 1A). The load was replaced on the wristband by the experimenter 3 s after the load-lifting (Figure 1C). No feedback was given to the participants regarding their performance, and importantly they were not aware of changes in their postural forearm position related to an acquisition process. We used the Presentation® (Neurobehavioral Systems) software for stimuli presentation.

Experimental conditions

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3 Two experimental conditions were proposed to the participant. Their order of presentation was
4 counterbalanced (session randomization) between participants to avoid any order effect. The first
5 experimental condition consisted in 8 blocks of 8 successive bimanual load-lifting trials (60 s of
6 passive rest between blocks) with a block-by-block increase in the delay separating the onset of load-
7 lifting from the fall of the load equipped on the postural arm (i.e., $\Delta t = +30$ ms by block, hence a 0 to
8 240 ms latency range from blocks 1 to 8). This was expected to place the participants in the
9 acquisition stage of motor learning, forcing them to constantly adjust across blocks the timing between
10 the onset of the load-lifting elbow flexion and the onset of the flexion inhibition on the postural arm
11 (ACQUISITION, 8 blocks of 8 trials for a total of 64 trials per participant). We voluntarily limited the
12 number of trials to 8 per block. Indeed, past experiments showed that adult participants reach a motor
13 performance plateau in postural stabilization after 8 to 12 trials (Schmitz and Assaiante 2002; Barlaam
14 et al. 2016). The second experimental condition consisted of 6 blocks of 10 trials (60 s of passive rest
15 between blocks). Since the load-lifting triggered the fall of the load suspended below the postural arm
16 with the shortest possible delay and this timing remained constant for each block (i.e., $\Delta t = 0$ s), we
17 were confident in the fact that a plateau would be reached at the end of the first block and that the
18 performance would be stabilized in the consecutive ones (CONTROL, 6 blocks of 10 trials for a total of
19 60 trials per participant).

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Data acquisition

Magnetoencephalography recordings were performed using a CTF-MEG system (CERMEP, France), with 275 radial gradiometers over the scalp and 33 reference channels for ambient field correction. MEG signals were digitalized at a sampling rate of 600 Hz and low-pass filtered (0–150 Hz). Head position was continuously recorded, using three head coils placed on the nasion and pre-auricular points prior to scanning. Brain MRI for co-registration with MEG data was recorded using a 3T Siemens Magnetom scanner (CERMEP, France – MAGNETOM Prisma, Siemens HealthCare), which computed 3D anatomical T1-weighted pictures covering the whole brain with 0.9 mm³ cubic voxels (TR: 3500 ms, TE: 2.24 ms). Extraction and projection of the individual cortical anatomy in the Montreal Neurologic Institute (MNI) template were respectively performed using Freesurfer

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3 (<http://freesurfer.net/>) and Brainstorm (Tadel et al. 2011), which is documented and freely available
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5 for download online under the GNU general public license (<http://neuroimage.usc.edu/brainstorm>).
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8 *Data recordings and analysis*

9 10 *Force plate measures*

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13 The onset of load-lifting was detected for both ACQUISITION and CONTROL as the first
14 deflection of the force signal transmitted by the force plate sensor, using a threshold function (CTF®
15 DataEditor software). Movement duration was defined as the time elapsed between the onset of load-
16 lifting and the first deflection of the force plate indicating the replacement of the load.
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22 *Elbow-joint upward rotation*

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25 Elbow-joint upward rotation after load-lifting was measured for all trials and conditions using
26 a high-frequency capacitive sensor (20 kHz, Figure 1B). For both ACQUISITION and CONTROL, the
27 first trial of each block was excluded to avoid readiness bias consecutive to the rest periods between
28 the blocks. This yielded to 56 trials analyzed in the ACQUISITION condition and 54 trials in the
29 CONTROL condition, and enabled to keep a balanced number of trials between the two experimental
30 conditions.
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38 *MEG data analysis*

39 40 *Sensor-level analysis*

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43 From previous MEG experiments carried on bimanual load-lifting, we investigated alpha (8-
44 12 Hz) and beta (13-30 Hz) frequencies (Ng et al. 2011, 2013a, b). Time-frequency power
45 distributions (0-40 Hz, Morelet wavelets) were normalized with reference to the 2.5 s baseline
46 preceding load-lifting (Z-score). Normalized time-frequency power distributions were then averaged
47 across sensors and trials, for each participant and each experimental condition. This yielded to i) by-
48 condition and ii) average (i.e., capturing the data from the two experimental conditions) time-
49 frequency power distributions. The average time-frequency power distribution in the sensors-space
50 was used to collect the time and frequency parameters corresponding to task-related changes in neural
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3 oscillations, i.e., event-related desynchronizations (ERD) and event-related synchronizations (ERS)
4 patterns (i.e., using a threshold of $|Z| > 2.00$, $p < 0.05$). These first steps prevented bias towards by-
5 condition differences during the following steps of the MEG data analysis.
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9 10 *Source reconstruction*

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12 Source reconstruction was obtained by applying a minimum norm inverse solution to MEG
13 gradiometer signals (Baillet et al. 2001), with constrained dipole orientation. For each trial, minimum
14 norm estimates yielded time windows from -2.5 to +3 s (relative to the load-lifting onset) of ongoing
15 cerebral activations, at each of the 5000 brain location corresponding to the nodes of participants'
16 tessellation. At each brain location of the individual tessellation, the source power was calculated in
17 the time-frequency window corresponding to the ERD and/or ERS patterns revealed by the sensor-
18 level analysis. Using a similar normalization procedure (i.e., Z-score against the 2.5 s baseline), the
19 normalized source power was projected in the MNI template. Since we were specifically interested in
20 brain sites controlling the acquisition phase of anticipatory postural adjustments, we built a random-
21 coefficient regression model with a by-subject and by-block random intercept. The model tested the
22 fixed effects of the EXPERIMENTAL CONDITION (i.e., ACQUISITION and CONTROL) and TRIAL
23 (i.e., numeric regressor), with an interaction term, on brain sources power within the specific time-
24 frequency window revealed by the sensor-level analysis. Brain locations where the two-way
25 interaction between EXPERIMENTAL CONDITION and TRIAL reached the statistical significance
26 threshold (see below) were selected as regions of interest (ROIs). This step of the MEG data analysis
27 enabled an objective and reproducible approach to the determination of the ROIs involved with the
28 acquisition of anticipatory postural adjustments.
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48 49 *Source analysis*

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51 Time course power peak amplitudes (i.e., corresponding to ERD and/or ERS) and their
52 latencies in each ROI were selected as the dependent variables of interest for both the ACQUISITION
53 and the CONTROL experimental conditions.
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58 59 *Statistical analyses*

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3 We used R (2018) and *nlme* (Pinheiro et al. 2014) to run a linear mixed effects analysis of i)
4 elbow-joint upward rotation and ii) MEG source parameters in each ROI (i.e., peak amplitudes and
5 latencies relative to the onset of load-lifting). For both analyses, we built random-coefficient
6 regression models with a by-subject and by-block random intercept. As fixed effects, we entered
7 EXPERIMENTAL CONDITION (i.e., ACQUISITION, CONTROL) and TRIAL (i.e., numeric regressor),
8 with an interaction term. Inspection of the residual plots did not reveal any obvious deviation from the
9 hypotheses of homoscedasticity or normality. The statistical significance threshold was set up for a
10 type 1 error rate of $\alpha = 5\%$. As effect sizes, we reported coefficients of determination (R-squared),
11 using the procedure for linear mixed effects models implemented in the *r2glmm* package (Edwards et
12 al. 2008; Jaeger et al. 2017). We also reported the statistical power ($p_{(1-\beta)}$) for statistically significant
13 effects and interactions from the functions implemented in the “*pwr*” package (Champely et al. 2018).
14 Post-hoc investigations of main and interaction effects were carried on using general linear hypotheses
15 testing of planned contrasts from the *multcomp* package (Hothorn et al. 2008; Bretz et al. 2016).
16 Holm’s sequential corrections were applied to control the false discovery rate (Holm 1979).
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33 Results

34 Behavioral data

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36 Movement duration ($M \pm CI_{95\%}$) was $1.48\text{ s} \pm 0.17$ during ACQUISITION and $1.53\text{ s} \pm 0.16$
37 during CONTROL. The linear mixed effect analysis revealed that elbow-joint upward rotation was
38 affected by the two-way interaction between EXPERIMENTAL CONDITION and TRIAL ($F_{(1, 1706)} =$
39 3.54 , $p < 0.05$, R-squared = 0.01, $p_{(1-\beta)} > 0.95$). As shown in Figure 2, the trial-to-trial decrease in
40 elbow-joint upward rotation was $0.03^\circ \pm 0.03$ higher during ACQUISITION ($-0.07^\circ \pm 0.01$) compared to
41 CONTROL (-0.04 ± 0.01) ($p < 0.05$).
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55 The elbow-joint upward rotation was also affected by the main effect of EXPERIMENTAL
56 CONDITION ($F_{(1, 1706)} = 116.01$, $p < 0.001$, R-squared = 0.06, $p_{(1-\beta)} > 0.95$) and TRIAL ($F_{(1, 1706)} =$
57 45.87 , $p < 0.001$, R-squared = 0.03, $p_{(1-\beta)} > 0.95$). Indeed, the elbow-joint upward rotation was
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3 0.41° ± 0.08 higher ($p < 0.001$) during ACQUISITION (4.07° ± 0.26) compared to CONTROL
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5 (3.65° ± 0.26), while the trial-to-trial decrease in elbow-joint rotation was -0.58° ± 0.02 ($p < 0.001$).
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8 *MEG data*

9 10 *Sensor-level analysis*

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13 Visual inspection of the time-frequency maps revealed ERD patterns in the alpha (8-12 Hz)
14 and beta (15-25 Hz) rhythms (Figure 3A). The beta ERD did not reach the statistical threshold ($|Z| =$
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16 1.5). By contrast, the alpha ERD exhibited a Z-score relative to the baseline of $|Z| > 2$ from -0.25 s to
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18 2.00 s relative to the onset of load-lifting (Figure 3A). The alpha rhythm (8-12 Hz) between 0.25 and
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20 2.00 s was thus considered the time-frequency window of interest for the forthcoming analyses.
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25 *** Insert Figure 3 about here ***
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27 *Source reconstruction*

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30 Brain generators of alpha oscillations from 0.25 s to 2.00 s relative to the load-lifting onset
31 during ACQUISITION and CONTROL (i.e., $|Z| > 2$) encompassed the primary motor and sensory cortices
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33 (BA1-3, BA4), as well as the premotor and parietal cortices (BA6) in both the motor (i.e., contralateral
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35 to the load-lifting arm) and postural (i.e., contralateral to the arm supporting the load) hemispheres
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37 (Figure 4A). Noteworthy, generators were more widely distributed within BA1-4 in the motor
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39 hemisphere during ACQUISITION compared to CONTROL (Figure 4A).
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46 *Source analysis*

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49 The linear mixed effects analysis carried on source alpha power between 0.25 s and 2.00 s
50 revealed that generators in the frontal cortex (BA10) of the motor (left) hemisphere and in the parietal
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52 cortex (BA7) of the postural (right) hemisphere were affected by the EXPERIMENTAL CONDITION
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54 by TRIAL interaction ($F_{(1, 1367)} = 11.91$, $p < 0.001$, R-squared = 0.008, $p_{(1-\beta)} = 0.91$; $F_{(1, 1367)} = 18.79$, p
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56 < 0.001 , R-squared = 0.01, $p_{(1-\beta)} = 0.96$, respectively). However, there was no main effect of
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58 EXPERIMENTAL CONDITION or TRIAL (i.e., both $p > 0.05$). As shown in Figure 5, the alpha
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3 power decrease across trials was $6.98 \% \pm 4.17$ higher during ACQUISITION ($-5.03 \% \pm 3.82$)
4 compared to CONTROL ($1.95 \% \pm 1.57$) in BA7 ($p < 0.001$). Likewise, in BA10 the alpha power
5 decrease across trials was $7.95 \% \pm 3.61$ higher during ACQUISITION ($-6.20 \% \pm 3.33$) compared to
6 CONTROL ($1.75 \% \pm 1.43$) ($p < 0.001$).
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12 *** Insert Figure 5 about here ***
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15 In the postural (right) hemisphere, the time course power in BA7 exhibited an ERD from -0.50
16 s to -0.10 s relative to the load-lifting onset, immediately followed by an ERS from 0.00 s to 0.35 s
17 (Figure 6). The linear mixed effects analysis carried on ERD peak amplitudes revealed a two-way
18 interaction between EXPERIMENTAL CONDITION and TRIAL ($F_{(1, 1367)} = 8.61$, $p < 0.01$, R-squared
19 = 0.007, $p_{(1-\beta)} = 0.87$), but there was no main effect of EXPERIMENTAL CONDITION or TRIAL
20 (i.e., both $p > 0.05$). The trial-to-trial decrease in ERD amplitudes was $17.26 \% \pm 11.89$ (relative to the
21 2.5 s baseline) during ACQUISITION ($-12.90 \% \pm 9.80$) compared to CONTROL ($4.35 \% \pm 4.71$) (Figure
22 6A). However, EXPERIMENTAL CONDITION and TRIAL did not affect the ERD peak latencies
23 (all $p > 0.05$). The two-way interaction between EXPERIMENTAL CONDITION and TRIAL also
24 affected ERS amplitudes ($F_{(1, 1367)} = 6.14$, $p = 0.01$, R-squared = 0.005, $p_{(1-\beta)} = 0.74$) but there was no
25 main effect of EXPERIMENTAL CONDITION and TRIAL (i.e., both $p > 0.05$). The trial-to-trial
26 increase in ERS amplitudes was reduced by $1.86 \% \pm 1.36$ during ACQUISITION ($1.63 \% \pm 1.25$)
27 compared to CONTROL ($0.22 \% \pm 0.54$).
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43 *** Insert Figure 6 about here ***
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46 In the motor (left) hemisphere, the time course power in BA10 exhibited an ERS from -0.30 s
47 relative to the onset of load-lifting to 0.35 s after, during both ACQUISITION and CONTROL (Figure
48 6B). The linear mixed effects analysis carried on ERS peaks revealed a two-way interaction between
49 EXPERIMENTAL CONDITION and TRIAL ($F_{(1, 1367)} = 12.11$, $p < 0.001$, R-squared = 0.009, $p_{(1-\beta)} >$
50 0.80). The decrease in ERS amplitudes across trials was $20.50 \% \pm 12.42$ higher during ACQUISITION
51 (-0.14 ± 0.11) compared to CONTROL (0.06 ± 0.03). The linear mixed effects analysis carried on ERS
52 latencies finally revealed no main effect or interaction (all $p > 0.05$).
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Discussion

The destabilizing effects of load-lifting on the forearm posture are rapidly foreseen in adults, due to the set-up of a proactive control that develops with practice during childhood (Paulignan et al. 1989; Schmitz and Assaiante 2002). The present study aimed at identifying brain correlates of the acquisition of anticipatory postural adjustments while learning a new sensorimotor coordination. We used a learning version of the bimanual load-lifting paradigm, in which we incrementally delayed the postural consequences of load-lifting. This placed the participants in a situation where the coordination between the right (load-lifting) arm and the left (postural) forearm kept requiring the acquisition of anticipatory postural adjustments. Conversely, under the CONTROL condition, the delay between the two events remained short and constant and the postural stabilization plateaued rapidly. The two experimental conditions were thus strictly identical, but one elicited an acquisition process through the update of the sensorimotor representation sustaining this new posture-movement coordination, and the other did not. It is noteworthy that, at the behavioral level, the two conditions only differed in terms of the amplitude of the left elbow upward rotation. Accordingly, small by-condition differences were expected, which was confirmed by the low effect sizes. While a sample size of sixteen healthy adult participants might mitigate against the generalization of the findings, the use of repeated measures enabled to achieve an acceptable statistical power, thus ensuring the potential reliability and reproducibility of the present findings (Button et al. 2013). The elbow-joint upward rotation measurement revealed a regular trial-to-trial decrease in the post-unloading movement maximal amplitude during ACQUISITION, hence providing behavioral evidence of the set-up of an anticipated postural control. No trial-to-trial decrease was recorded under CONTROL. Elbow-joint upward rotation was overall reduced during CONTROL compared to ACQUISITION, hence attesting a more efficient postural control. Importantly, the implicit nature of this acquisition rules out any potential attentional bias.

Previous functional brain imaging research on bimanual load-lifting emphasized pre-lifting brain activations, and used sliding time windows to investigate the brain correlates of already learned anticipatory postural adjustments (e.g., Ng et al. 2011, 2013a, b). Here, we were specifically interested

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3 in the acquisition process. Voluntary motor commands are systematically duplicated into an efferent
4 copy predicting the sensory consequence of the action, i.e., forward modeling. Forward predictive
5 models are continuously referred to the sensory afferents generated by the movement. Detection of
6 errors enables online corrections through feedback/feedforward loops (Wolpert and Ghahramani 2000;
7 Wolpert and Flanagan 2001; Grush 2004). In other words, errors enable the refinement of the forward
8 predictive model, which can be further converted into updates of the internal representation
9 associating the goal of the movement with the motor commands required to achieve that goal, i.e.,
10 inverse model. The forward predictive model, which would capture the causal relationship between the
11 action and its postural outcome to progressively refine the sensory prediction, was advanced as the
12 primary account to the acquisition of anticipatory postural adjustments in the learning version of the
13 bimanual load-lifting paradigm (Barlaam et al. 2016).

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27 The sensor-level analysis revealed comparable patterns of time-frequency power distributions
28 during ACQUISITION and CONTROL. Power variations in brain oscillations were present in the alpha (8-
29 12 Hz) and beta (13-35 Hz) frequency rhythms, but only the alpha ERD reached the statistical
30 threshold. Given their topographical distribution, changes in alpha oscillations correspond to the
31 sensorimotor mu rhythm associated with motor behaviors (Pfurtscheller 2003). Source reconstruction
32 of mu generators revealed comparable activation patterns during ACQUISITION and CONTROL. We did
33 not expect a distinct spatial distribution of the cortical ERD generators between ACQUISITION and
34 CONTROL since the conditions only differed in terms of delayed timing between the load-lifting and its
35 postural consequences. Cortical generators involved the premotor and sensorimotor cortices as well as
36 the posterior parietal cortex in both hemispheres. These results largely corroborate past observations
37 (Kazennikov et al. 2006; Ng et al. 2011, 2013a, b). Interestingly, the spatial distribution of the mu
38 generators in the motor hemisphere encompassed a broader surface of the cortical tessellation during
39 ACQUISITION as compared to CONTROL. The reduced involvement of neural resources has been
40 associated with greater neural efficiency and represents a neurophysiological correlate of the motor
41 expertise (e.g., Krings et al. 2000; Kita et al. 2001; Del Percio et al. 2008; Wright et al. 2012).
42 ACQUISITION and CONTROL represent different levels of skill expertise during the learning of a new
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3 bimanual coordination. This was reflected at the brain level by more refined and circumscribed
4 activation patterns in central regions of the motor hemisphere (i.e., BA1-4) during CONTROL compared
5 to ACQUISITION. The source reconstruction thus underlined neurophysiological correlates associated
6 with two distinct levels of expertise. More precisely, these may correspond to the acquisition and
7 motor performance plateau underlined in motor learning frameworks (Schmidt et al. 2018), or to the
8 fast and slow stages of performance improvements preceding automation (Doyon et al. 2011, for an
9 overview).

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19 In order to investigate the neural structures specifically involved with the acquisition of
20 anticipatory postural adjustments, we performed regression analyses to specifically disclose the brain
21 sites exhibiting a distinct profile of trial-to-trial response during ACQUISITION compared to CONTROL.
22 These analyses unveiled specific activities within BA10 (in the left hemisphere) and BA7 (in the right
23 hemisphere). At the quantitative level, BA10 and BA7 both exhibited a decreased activation across
24 trials during ACQUISITION but increased activation, i.e., decreased power attesting neural
25 desynchronization (Pfurtscheller and Lopes da Silva 1999) during CONTROL. This suggests that both
26 regions participate to the update of the internal representation of the new bimanual load-lifting
27 coordination, i.e., the central integration of the expected postural consequences of the movement,
28 based on the trial-to-trial detection of errors between the efference copy and the actual consequences
29 of load-lifting. BA7 is part of the parietal cortex, which is generally known to be involved in the
30 generation, maintenance and update of internal models (Wolpert et al. 1998; Blakemore and Sirigu
31 2003). The source reconstruction enabled to specify the location of the source on the medial surface of
32 the superior parietal cortex, corresponding to the precuneus. The precuneus is thought to be a key
33 region for the maintenance and update of egocentric representations during self-motion (Land 2014).
34 In the bimanual load-lifting task, the forearm posture serves as a reference frame for the manipulation
35 of objects and is stabilized by the anticipatory postural adjustments (Massion et al., 1999). Hence,
36 during the acquisition process, this egocentric reference frame has to be updated along with the
37 upward elbow rotation decrease and this is achieved through the involvement of the precuneus. The
38 specificity of the involvement of this region in the acquisition of new postural adjustments finds
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3 another argument in the fact that its lateralization in the right parietal cortex is contralateral to the
4 postural forearm. On the other hand, the prefrontal cortex, and specifically its medial portion
5 corresponding to BA10, is known to play a key role during motor learning, specifically the refinement
6 of the parameters of the motor coordination underlying adjustment of the motor performance. Yet,
7 while both the precuneus and BA10 emerged as ROIs for the acquisition of anticipatory postural
8 adjustments, these regions may not play a key role during the central processing of inverse models
9 refined as a result of practice as attested by the decreased activation along with trials repetition during
10 CONTROL.

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21 At the qualitative level, analyzing the time-course of the mu power in the medial prefrontal
22 cortex of the left hemisphere revealed that ERS amplitudes during ACQUISITION decreased along with
23 practice, and progressively geared towards the pattern observed during CONTROL. It thus indicates that
24 decreased BA10 inhibition after load-lifting can be associated with the acquisition of anticipatory
25 postural adjustments during bimanual load-lifting. Considering the well-established role of the medial
26 prefrontal cortex in behavioral adjustments resulting from ongoing motor learning (Ridderinkhof et al.
27 2004), this might account for a more efficient management of the mental load during bimanual load-
28 lifting. Albeit speculative, more efficient processing of the anticipatory postural adjustments through
29 forward modeling might decrease the future need to inhibit this region to reallocate neural resources to
30 post-unloading operations, such as the inhibition of the left forearm flexor muscle and the refinement
31 of the forward predictive model based on the error detection. Noteworthy, the precuneus in the right,
32 postural hemisphere exhibited a distinct pattern of time-course power distributions. The post-
33 unloading ERS was preceded by an ERD preliminary to the onset of load-lifting. Again, the ERD
34 amplitude decreased along with trial repetition during ACQUISITION and progressively matched the
35 response pattern observed during CONTROL. It thus suggests that increased precuneus activation can
36 be associated with the acquisition of anticipatory postural adjustments through the update of the
37 postural reference frame until it is stabilized. This adds to a large body of research the role of the
38 parietal cortex in cognitive processes associated with motor update (Wolpert et al. 1998; Blakemore
39 and Sirigu 2003). Interestingly, the latencies of both ERS and ERD response patterns were similar
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3 during ACQUISITION and CONTROL. This indicates that the timing of power changes in neural
4 oscillations did not predict the acquisition of anticipatory postural adjustments in this task. Differences
5 in the timing of neural activities, specifically those recorded within primary sensorimotor brain
6 regions, might rather represent a neural signature of distinct expertise levels during bimanual load-
7 lifting.
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14 Overall, the data support a more efficient management of neural resources within brain regions
15 involved in the central processing of voluntary and anticipatory motor command signals during the
16 acquisition of anticipatory postural adjustments. Our results emphasize the specific role of the
17 precuneus and of the medial prefrontal cortex in the acquisition process, which invalidates our initial
18 working hypothesis, based on previous studies (Donchin et al. 1998; Ioffe et al. 2003; Kazennikov et
19 al. 2006, 2007, 2008), that the primary motor cortex would be a core region supporting the acquisition
20 of the coordination in this task. However, as shown by the spatial distribution of the generators of the
21 mu rhythm during ACTIVATION and CONTROL, the degree of primary sensorimotor cortex involvement
22 appeared to reflect the expertise level, hence the current motor learning state but not did not appear to
23 play a role in the acquisition stage. According to the emulation theory (Grush 2004), sensory
24 consequences of voluntary movements can be used to co-program motor outputs and foresee the
25 expected perturbations. During development, the efficient stabilization of the postural forearm requires
26 mastering the timing of the forearm flexor muscle inhibition, which must be synchronized with the
27 timing of the load lifting (Schmitz et al. 2002). Past experiments compared voluntary and imposed
28 load-lifting conditions to identify brain structures controlling the anticipated postural adjustments of
29 the left forearm (Kazennikov et al. 2008; Ng et al. 2011, 2013a, b). The present data extend past
30 findings by examining brain activities mediating the acquisition of anticipated postural adjustments
31 during bimanual load-lifting. It provides neurophysiological insights on the early hypothesis by
32 Berrigan and Simoneau (2007) that the brain could capture new temporal relationships between an
33 action and its consequences on posture. The MEG analysis disclosed frontal and parietal structures,
34 more specifically the precuneus in the postural hemisphere and the medial prefrontal cortex in the
35 motor hemisphere. Specific patterns of time-course power distributions within these two regions were
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3 associated with the acquisition of anticipatory postural adjustments. Decreased post-unloading
4 inhibition of the left medial prefrontal cortex and increased pre-unloading activation of the right
5 precuneus were recorded along with trial repetition during ACQUISITION. The data extends current
6 knowledge regarding the brain correlates of bimanual load-lifting, and underlines the specific
7 involvement of associative cortical regions, but not primary sensorimotor regions, during the
8 acquisition of anticipatory postural adjustments.
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For Peer Review

Acknowledgments

The authors declare no conflict of interest.

This study was supported by funding from the French National Research Agency: ANR SaMenta ASD-BARN (ANR-12-SAMA-015-01), LABEX CORTEX (ANR-11-LABX-0042) of Université de Lyon, within the program "Investissements d'Avenir" (ANR-11-IDEX-0007).

We gratefully acknowledge CC-IN2P3 through TIDRA (<http://www.tidra.org>) for providing a significant amount of the computing resources and services needed for this work.

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Figure legends

Figure 1. A. Bimanual load-lifting coordination involving i) the unloading (right) arm and ii) the postural (left) arm. The voluntary lift-up the 850 g load (1) triggered the fall of the load fixed to the postural arm (2) B. Elbow-joint stabilization and measurement of elbow-joint flexion. C. Timing of a bimanual load-lifting trial.

Figure 2. EXPERIMENTAL CONDITION by TRIAL effect (fitted estimates) on elbow-joint upward rotation. Regression slopes are represented with $CI_{95\%}$ (dotted lines). During ACQUISITION, each block involved new timing parameters between the voluntary and anticipatory motor command signals addressed to the right and left upper limbs, respectively. During CONTROL, the timing between the voluntary and anticipatory motor command signals required to achieve efficient forearm stabilization post-unloading remained unchanged. * $p < 0.05$.

Figure 3. A. Averaged (group level) time-frequency power distributions (-2.5 s – 3 s) relative to the onset of load-lifting during ACQUISITION and CONTROL. B. Averaged (group level) time-frequency power distributions (-2.5 s – 3 s) capturing the data from both experimental conditions (left panel). The alpha (8-12 Hz, $|Z| > 2$) and beta (13-35 Hz, $|Z| < 2$) ERD elicited by the bimanual load-lifting task (red and blue dotted squares, respectively). Averaged topographical distributions (group level) of alpha power (8-12 Hz, 0.25-2.00 s) in the sensors space capturing the data from both experimental conditions (right panel).

Figure 4. A. Spatial distributions of generators of alpha power (8-12 Hz, 0.25-2.00 s) in the source space, as revealed by the source reconstruction step of the MEG data analysis (see Methods). B. Regions of interest resulting from the linear mixed-effects analysis of the two-way interaction between EXPERIMENTAL CONDITION and TRIAL carried on source power within the time-frequency window of interest, as revealed by the sensor-level analysis (8-12 Hz, 0.25-2.00 s, see sensors-level analysis).

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3 Figure 5. EXPERIMENTAL CONDITION by TRIAL interaction effect (fitted estimates) on
4 source power within the time-frequency window of interest (8-12 Hz, 0.25-2.00 s) in the two regions
5 of interest. *** $p < 0.001$.
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10 Figure 6. A. Averaged time-course of source alpha power (8-12 Hz) in BA7 (left panel)
11 exhibiting an ERD from -0.50 s to -0.10 s (grey shades) relative to the onset of load-lifting. Blue and
12 red shades correspond to $CI_{95\%}$. EXPERIMENTAL CONDITION by TRIAL interaction effect (fitted
13 estimates) on the BA7 ERD amplitudes (right panel). Regression slopes are represented with $CI_{95\%}$
14 (dotted lines). B. Averaged time-course of source alpha power (8-12 Hz) in BA10 (left panel)
15 exhibiting an ERS from -0.30 s to 0.35 s (grey shades) relative to the onset of load-lifting. Blue and
16 red shades correspond to $CI_{95\%}$. EXPERIMENTAL CONDITION by TRIAL interaction effect (fitted
17 estimates) on the BA10 ERS amplitudes (right panel). Regression slopes are represented with $CI_{95\%}$
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References

- 1
2
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4
5
6 Adams JA (1987) Historical review and appraisal of research on the learning, retention, and transfer of
7 human motor skills. *Psychological Bulletin* 101:41–74. doi: 10.1037/0033-2909.101.1.41
8
9 Baillet S, Mosher JC, Leahy RM (2001) Electromagnetic brain mapping. *IEEE Signal processing*
10 *magazine* 18:14–30
11
12 Barlaam F, Fortin C, Vaugoyeau M, et al (2012) Development of action representation during
13 adolescence as assessed from anticipatory control in a bimanual load-lifting task.
14 *Neuroscience* 221:56–68. doi: 10.1016/j.neuroscience.2012.06.062
15
16 Barlaam F, Vaugoyeau M, Fortin C, et al (2016) Shift of the Muscular Inhibition Latency during On-
17 Line Acquisition of Anticipatory Postural Adjustments. *PLoS One* 11:. doi:
18 10.1371/journal.pone.0154775
19
20 Berrigan F, Simoneau M (2007) Is the brain able to capture a new temporal relationship between a
21 motor action and its consequence? *Exp Brain Res* 181:321–332. doi: 10.1007/s00221-007-
22 0929-9
23
24 Blakemore S-J, Sirigu A (2003) Action prediction in the cerebellum and in the parietal lobe. *Exp Brain*
25 *Res* 153:239–245. doi: 10.1007/s00221-003-1597-z
26
27 Bouisset S, Zattara M (1981) A sequence of postural movements precedes voluntary movement.
28 *Neuroscience Letters* 22:263–270. doi: 10.1016/0304-3940(81)90117-8
29
30 Bretz F, Westfall P, Hothorn T (2016) Multiple comparisons using R. Chapman and Hall/CRC
31
32 Button KS, Ioannidis JPA, Mokrysz C, et al (2013) Power failure: why small sample size undermines
33 the reliability of neuroscience. *Nature Reviews Neuroscience* 14:365–376. doi:
34 10.1038/nrn3475
35
36 Champely S, Ekstrom C, Dalgaard P, et al (2018) Package ‘pwr’
37
38 Dayan E, Cohen LG (2011) Neuroplasticity subserving motor skill learning. *Neuron* 72:443–454. doi:
39 10.1016/j.neuron.2011.10.008
40
41 Del Percio C, Rossini PM, Marzano N, et al (2008) Is there a “neural efficiency” in athletes? A high-
42 resolution EEG study. *NeuroImage* 42:1544–1553. doi: 10.1016/j.neuroimage.2008.05.061
43
44 Donchin O, Gribova O, Steinberg O, et al (1998) Primary motor cortex is involved in bimanual
45 coordination
46
47 Doyon J, Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor
48 skills. *Current Opinion in Neurobiology* 15:161–167. doi: 10.1016/j.conb.2005.03.004
49
50 Doyon J, Orban P, Barakat M, et al (2011) [Functional brain plasticity associated with motor
51 learning]. *Med Sci (Paris)* 27:413–420. doi: 10.1051/medsci/2011274018
52
53 Doyon J, Penhune V, Ungerleider LG (2003) Distinct contribution of the cortico-striatal and cortico-
54 cerebellar systems to motor skill learning. *Neuropsychologia* 41:252–262. doi:
55 10.1016/S0028-3932(02)00158-6
56
57 Doyon J, Song AW, Karni A, et al (2002) Experience-dependent changes in cerebellar contributions to
58 motor sequence learning. *PNAS* 99:1017–1022. doi: 10.1073/pnas.022615199
59
60

- 1
2
3 Dufossé M, Hugon M, Massion J (1985) Postural forearm changes induced by predictable in time or
4 voluntary triggered unloading in man. *Exp Brain Res* 60:330–334
5
- 6 Dufossé M, Hugon M, Massion J, Paulignan Y (1987) Bimanual Load-Lifting Task. A Model for the
7 Study of Coordination Between Posture and Movement. In: Struppler A, Weindl A (eds)
8 Clinical Aspects of Sensory Motor Integration. Springer Berlin Heidelberg, pp 297–304
9
- 10 Edwards LJ, Muller KE, Wolfinger RD, et al (2008) An R2 Statistic for Fixed Effects in the Linear
11 Mixed Model. *Stat Med* 27:6137–6157. doi: 10.1002/sim.3429
12
- 13 Grush R (2004) The emulation theory of representation: motor control, imagery, and perception.
14 *Behav Brain Sci* 27:377–396; discussion 396-442
15
- 16 Hardwick RM, Rottschy C, Miall RC, Eickhoff SB (2013) A quantitative meta-analysis and review of
17 motor learning in the human brain. *Neuroimage* 67:283–297. doi:
18 10.1016/j.neuroimage.2012.11.020
19
- 20 Holm S (1979) A simple sequentially rejective multiple test procedure. *Scandinavian journal of*
21 *statistics* 65–70
22
- 23 Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J*
24 50:346–363. doi: 10.1002/bimj.200810425
25
- 26 Hugon M, Massion J, Wiesendanger M (1982) Anticipatory postural changes induced by active
27 unloading and comparison with passive unloading in man. *Pflügers Archiv* 393:292–296. doi:
28 10.1007/BF00581412
29
- 30 Ioffe ME, Massion J, Schmitz C, et al (2003) Specific Functions of the Motor Cortex in Reorganizing
31 Coordinations during Motor Training in Animals and Humans. *Neurosci Behav Physiol*
32 33:143–150. doi: 10.1023/A:1021717829999
33
- 34 Jaeger BC, Edwards LJ, Das K, Sen PK (2017) An R2 statistic for fixed effects in the generalized
35 linear mixed model. *Journal of Applied Statistics* 44:1086–1105. doi:
36 10.1080/02664763.2016.1193725
37
- 38 Kazennikov O, Solopova I, Talis V, Ioffe M (2008) Anticipatory postural adjustment: the role of
39 motor cortex in the natural and learned bimanual unloading. *Experimental Brain Research*
40 186:215–223. doi: 10.1007/s00221-007-1224-5
41
- 42 Kazennikov OV, Solopova IA, Talis VL, et al (2006) Involvement of the Motor Cortex in the
43 Bimanual Unloading Reaction: A Transcranial Magnetic Stimulation Study. *Neuroscience and*
44 *Behavioral Physiology* 36:177–183. doi: 10.1007/s11055-005-0176-0
45
- 46 Kazennikov OV, Solopova IA, Talis VL, Ioffe ME (2007) Anticipatory postural adjustment before
47 bimanual unloading reactions: The role of the motor cortex in motor learning. *Neuroscience*
48 *and Behavioral Physiology* 37:651–657. doi: 10.1007/s11055-007-0065-9
49
- 50 Kita Y, Mori A, Nara M (2001) Two types of movement-related cortical potentials preceding wrist
51 extension in humans. *Neuroreport* 12:2221–2225
52
- 53 Krings T, Töpper R, Foltys H, et al (2000) Cortical activation patterns during complex motor tasks in
54 piano players and control subjects. A functional magnetic resonance imaging study.
55 *Neuroscience Letters* 278:189–193. doi: 10.1016/S0304-3940(99)00930-1
56
- 57 Land MF (2014) Do we have an internal model of the outside world? *Philos Trans R Soc Lond B Biol*
58 *Sci* 369:. doi: 10.1098/rstb.2013.0045
59
60

- 1
2
3 Lee TD (1988) Chapter 7 Transfer-Appropriate Processing: A Framework for Conceptualizing
4 Practice Effects in Motor Learning. In: Meijer OG, Roth K (eds) *Advances in Psychology*.
5 North-Holland, pp 201–215
6
- 7 Luft AR, Buitrago MM (2005) Stages of motor skill learning. *Molecular Neurobiology* 32:205–216.
8 doi: 10.1385/MN:32:3:205
9
- 10 Massion J (1992) Movement, posture and equilibrium: Interaction and coordination. *Progress in*
11 *Neurobiology* 38:35–56. doi: 10.1016/0301-0082(92)90034-C
12
- 13 Massion J, Ioffe M, Schmitz C, et al (1999) Acquisition of anticipatory postural adjustments in a
14 bimanual load-lifting task: normal and pathological aspects. *Experimental Brain Research*
15 128:229–235. doi: 10.1007/s002210050842
16
- 17 Ng THB, Sowman PF, Brock J, Johnson BW (2011) Premovement brain activity in a bimanual load-
18 lifting task. *Exp Brain Res* 208:189–201. doi: 10.1007/s00221-010-2470-5
19
- 20 Ng THB, Sowman PF, Brock J, Johnson BW (2013a) Neuromagnetic brain activity associated with
21 anticipatory postural adjustments for bimanual load lifting. *NeuroImage* 66:343–352. doi:
22 10.1016/j.neuroimage.2012.10.042
23
- 24 Ng THB, Sowman PF, Brock J, Johnson BW (2013b) Neuromagnetic imaging reveals timing of
25 volitional and anticipatory motor control in bimanual load lifting. *Behavioural Brain Research*
26 247:182–192. doi: 10.1016/j.bbr.2013.03.020
27
- 28 Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory.
29 *Neuropsychologia* 9:97–113. doi: 10.1016/0028-3932(71)90067-4
30
- 31 Paulignan Y, Dufossé M, Hugon M, Massion J (1989) Acquisition of co-ordination between posture
32 and movement in a bimanual task. *Experimental Brain Research* 77:337–348. doi:
33 10.1007/BF00274991
34
- 35 Pfuertscheller G (2003) Induced Oscillations in the Alpha Band: Functional Meaning. *Epilepsia* 44:2–8.
36 doi: 10.1111/j.0013-9580.2003.12001.x
37
- 38 Pfuertscheller G, Lopes da Silva FH (1999) Event-related EEG/MEG synchronization and
39 desynchronization: basic principles. *Clin Neurophysiol* 110:1842–1857
40
- 41 Pinheiro J, Bates D, DebRoy S, Sarkar D (2014) Linear and nonlinear mixed effects models. R
42 package version 3:
43
- 44 Rémy F, Wenderoth N, Lipkens K, Swinnen SP (2010) Dual-task interference during initial learning
45 of a new motor task results from competition for the same brain areas. *Neuropsychologia*
46 48:2517–2527. doi: 10.1016/j.neuropsychologia.2010.04.026
47
- 48 Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S (2004) The Role of the Medial Frontal
49 Cortex in Cognitive Control. *Science* 306:443–447. doi: 10.1126/science.1100301
50
- 51 Rueda-Delgado LM, Solesio-Jofre E, Serrien DJ, et al (2014) Understanding bimanual coordination
52 across small time scales from an electrophysiological perspective. *Neuroscience &*
53 *Biobehavioral Reviews* 47:614–635. doi: 10.1016/j.neubiorev.2014.10.003
54
- 55 Schmidt RA, Lee T, Winstein C, et al (2018) *Motor Control and Learning*, 6E. Human kinetics
56
57
58
59
60

- 1
2
3 Schmitz C, Assaiante C (2002) Developmental sequence in the acquisition of anticipation during a
4 new co-ordination in a bimanual load-lifting task in children. *Neuroscience Letters* 330:215–
5 218. doi: 10.1016/S0304-3940(02)00590-6
6
7 Schmitz C, Martin N, Assaiante C (2002) Building anticipatory postural adjustment during childhood:
8 a kinematic and electromyographic analysis of unloading in children from 4 to 8 years of age.
9 *Experimental Brain Research* 142:354–364. doi: 10.1007/s00221-001-0910-y
10
11 Seidler RD (2010) Neural correlates of motor learning, transfer of learning, and learning to learn.
12 *Exercise and sport sciences reviews* 38:3
13
14 Tadel F, Baillet S, Mosher JC, et al (2011) Brainstorm: A User-Friendly Application for MEG/EEG
15 Analysis. In: *Computational Intelligence and Neuroscience*.
16 <https://www.hindawi.com/journals/cin/2011/879716/cta/>. Accessed 19 Jan 2019
17
18 Team RC (2018) R: A Language and Environment for Statistical Computing, R Foundation for
19 Statistical Computing, Austria, 2015. ISBN 3-900051-07-0: URL <http://www.R-project.org>
20
21 Ungerleider LG, Doyon J, Karni A (2002) Imaging brain plasticity during motor skill learning.
22 *Neurobiol Learn Mem* 78:553–564
23
24 Wolpert DM, Flanagan JR (2001) Motor prediction. *Curr Biol* 11:R729-732
25
26 Wolpert DM, Ghahramani Z (2000) Computational principles of movement neuroscience. *Nature*
27 *Neuroscience* 3:1212–1217. doi: 10.1038/81497
28
29 Wolpert DM, Goodbody SJ, Husain M (1998) Maintaining internal representations: the role of the
30 human superior parietal lobe. *Nat Neurosci* 1:529–533. doi: 10.1038/2245
31
32 Wright DJ, Holmes P, Di Russo F, et al (2012) Reduced Motor Cortex Activity during Movement
33 Preparation following a Period of Motor Skill Practice. *PLoS One* 7:. doi:
34 10.1371/journal.pone.0051886
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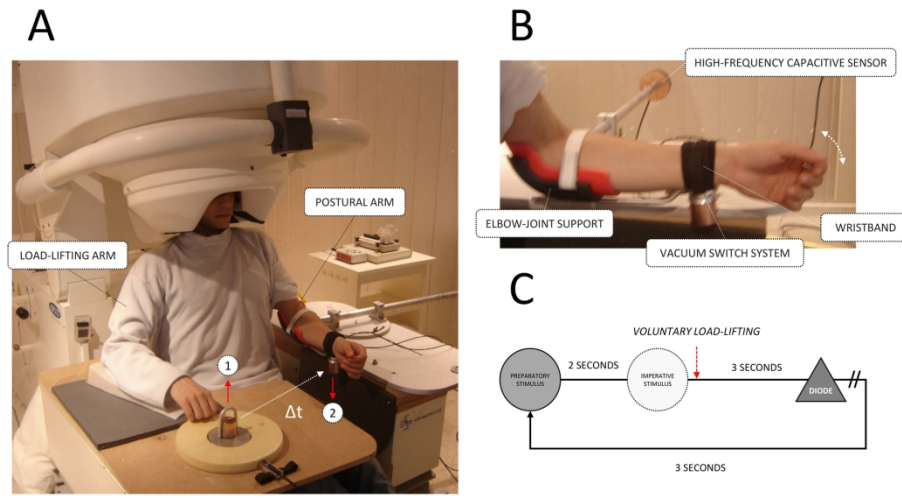


Figure 1. A. Bimanual load-lifting coordination involving i) the unloading (right) arm and ii) the postural (left) arm. The voluntary lift-up the 850 g load (1) triggered the fall of the load fixed to the postural arm (2) B. Elbow-joint stabilization and measurement of elbow-joint flexion. C. Timing of a bimanual load-lifting trial.

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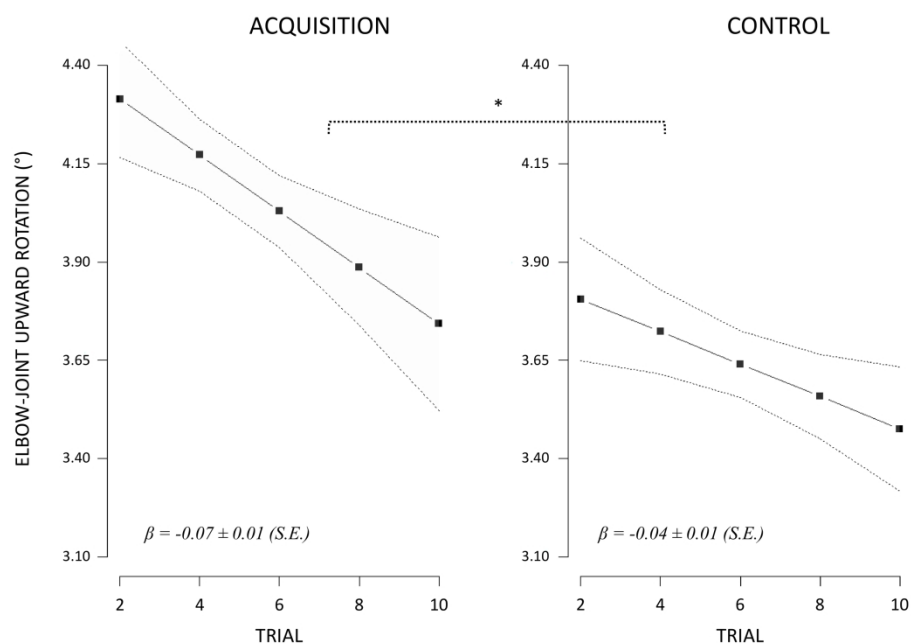


Figure 2. EXPERIMENTAL CONDITION by TRIAL effect (fitted estimates) on elbow-joint upward rotation. Regression slopes are represented with CI95% (dotted lines). During ACQUISITION, each block involved new timing parameters between the voluntary and anticipatory motor command signals addressed to the right and left upper limbs, respectively. During CONTROL, the timing between the voluntary and anticipatory motor command signals required to achieve efficient forearm stabilization post-unloading remained unchanged. * $p < 0.05$.

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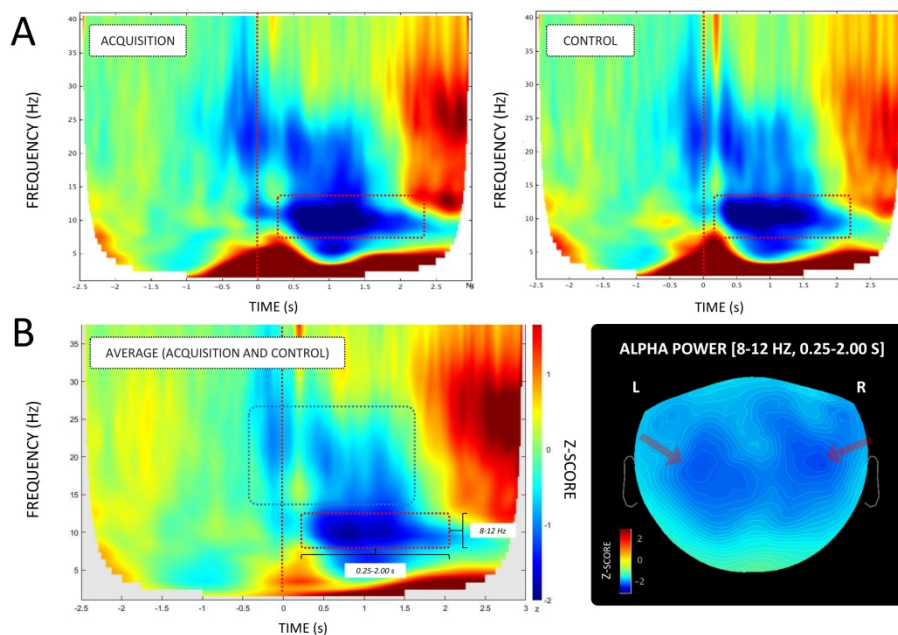


Figure 3. A. Averaged (group level) time-frequency power distributions (-2.5 s – 3 s) relative to the onset of load-lifting during ACQUISITION and CONTROL. B. Averaged (group level) time-frequency power distributions (-2.5 s – 3 s) capturing the data from both experimental conditions (left panel). The alpha (8-12 Hz, $|Z| > 2$) and beta (13-35 Hz, $|Z| < 2$) ERD elicited by the bimanual load-lifting task (red and blue dotted squares, respectively). Averaged topographical distributions (group level) of alpha power (8-12 Hz, 0.25-2.00 s) in the sensors space capturing the data from both experimental conditions (right panel).

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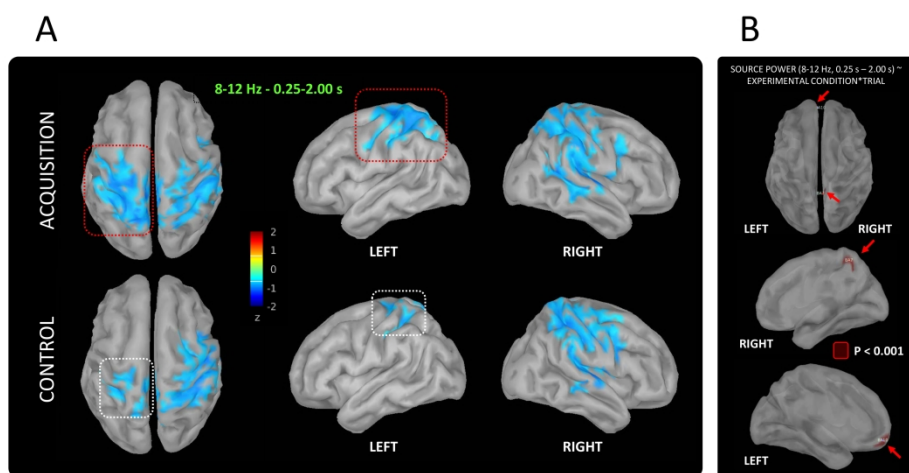


Figure 4. Spatial distributions of generators of alpha power (8-12 Hz, 0.25-2.00 s) in the source space, as revealed by the source reconstruction step of the MEG data analysis (see Methods). B. Regions of interest resulting from the linear mixed-effects analysis of the two-way interaction between EXPERIMENTAL CONDITION and TRIAL carried on source power within the time-frequency window of interest, as revealed by the sensor-level analysis (8-12 Hz, 0.25-2.00 s, see sensors-level analysis).

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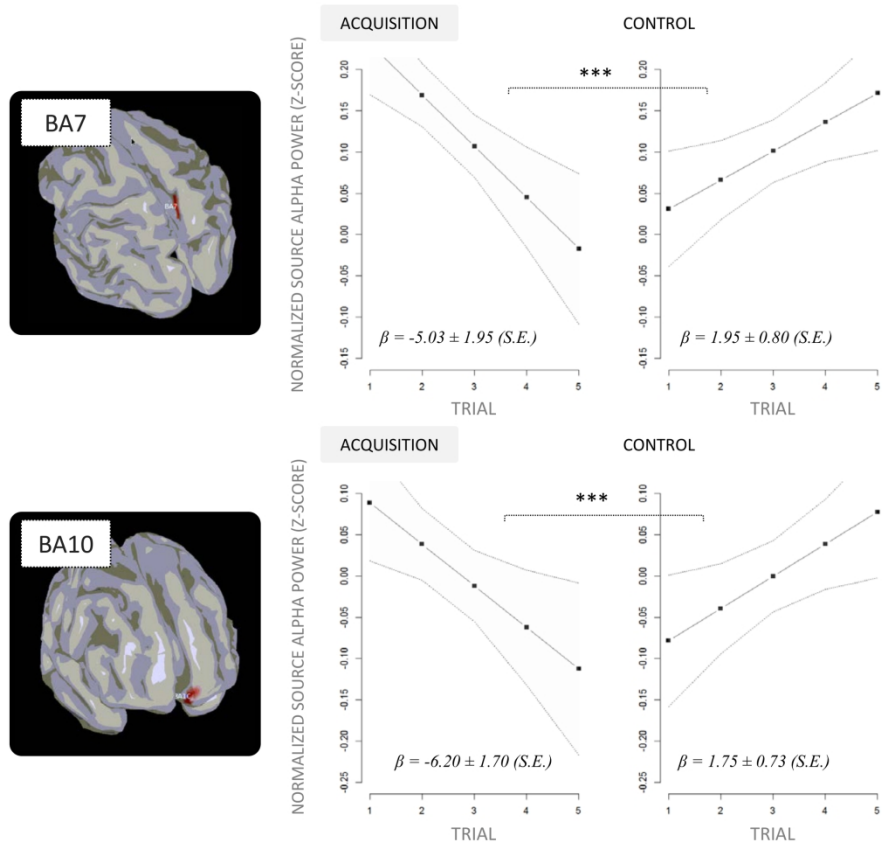


Figure 5. EXPERIMENTAL CONDITION by TRIAL interaction effect (fitted estimates) on source power within the time-frequency window of interest (8-12 Hz, 0.25-2.00 s) in the two regions of interest. ***p < 0.001.

213x189mm (300 x 300 DPI)

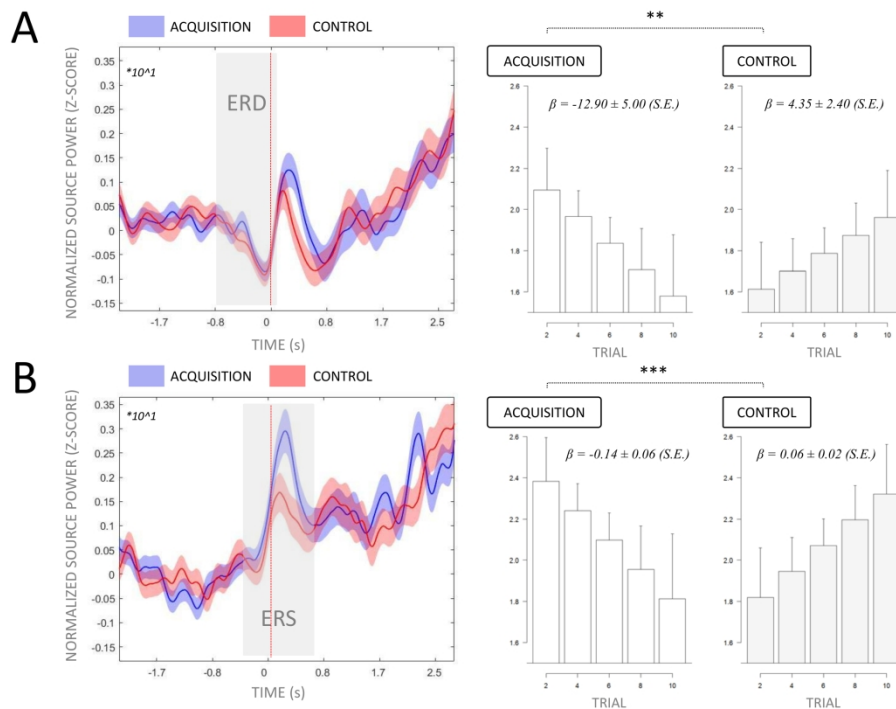


Figure 6. A. Averaged time-course of source alpha power (8-12 Hz) in BA7 (left panel) exhibiting an ERD from -0.50 s to -0.10 s (grey shades) relative to the onset of load-lifting. Blue and red shades correspond to CI95%. EXPERIMENTAL CONDITION by TRIAL interaction effect (fitted estimates) on the BA7 ERD amplitudes (right panel). Regression slopes are represented with CI95% (dotted lines). B. Averaged time-course of source alpha power (8-12 Hz) in BA10 (left panel) exhibiting an ERS from -0.30 s to 0.35 s (grey shades) relative to the onset of load-lifting. Blue and red shades correspond to CI95%. EXPERIMENTAL CONDITION by TRIAL interaction effect (fitted estimates) on the BA10 ERS amplitudes (right panel). Regression slopes are represented with CI95% (dotted lines)

259x190mm (300 x 300 DPI)