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ABBREVIATED TITLE: Mu rhythm crossmodal multivariate classification

Crossmodal classification of mu rhythm activity during action observation and execution suggests specificity to somatosensory features of actions.

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Abstract

The alpha mu rhythm (8-13 Hz) has been considered to reflect mirror neuron activity due to the fact that it is attenuated by both action observation and action execution. The putative link between mirror neuron system activity and the mu rhythm has been used to study the involvement of the mirror system in a wide range of socio-cognitive processes and clinical disorders. However, previous research has failed to convincingly demonstrate the specificity of the mu rhythm, meaning that it is unclear whether the mu rhythm reflects mirror neuron activity. It also remains unclear if mu rhythm suppression during action observation reflects the processing of motor or tactile information. In an attempt to assess the validity of the mu rhythm as a measure of mirror neuron activity, we used crossmodal pattern classification to assess the specificity of EEG mu rhythm response to action varying in terms of action type (whole-hand or precision grip), concurrent tactile stimulation (stimulation or no stimulation), or object use (transitive or intransitive actions) in twenty human participants. The main results reveal that above-chance crossmodal classification of mu rhythm activity was obtained in the central channels for tactile stimulation and action transitivity but not for action type. Furthermore, traditional univariate analyses applied to the same data were insensitive to differences between conditions. By calling into question the relationship between mirror system activity and the mu rhythm, these results have important implications for the use and interpretation of mu rhythm activity.

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Significance statement

The central alpha mu rhythm oscillation is a widely used measure of the human mirror neuron system that has been used to make important claims concerning cognitive functioning in health and in disease. Here, we used a novel multivariate analytical approach to show that crossmodal EEG mu rhythm responses primarily index the somatosensory features of actions, suggesting that the mu rhythm is not a valid measure of mirror neuron activity. Results may lead to the revision of the conclusions of many previous studies using this measure, and to the transition towards a theory of mu rhythm function that is more consistent with current models of sensory processing in the self and in others.

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Introduction

Mirror neurons (MN), firing both during the observation and execution of actions (di Pellegrino et al., 1992), have been suggested to contribute to the understanding of others' action by matching observed actions to one's own neural code to perform that action (Gallese et al., 1996). MN activity is notoriously difficult to measure non-invasively in humans given the limited spatial resolution of human neuroimaging techniques (Dinstein et al., 2008). Despite these methodological constraints, many have argued for the involvement of MN in a variety of phenomena using neuroimaging measures such as the EEG central alpha mu rhythm.

The alpha mu rhythm (8-13 Hz, henceforth "mu rhythm") is an oscillation measured over sensorimotor areas that is attenuated both during the observation and execution of actions (see Fox et al., 2015). On the basis of this similar response during action observation and execution, the mu rhythm has been considered to index MN activity (Pineda, 2005; Fox et al., 2015). As a consequence, it has been used by many researchers to suggest the involvement of MN throughout development in processes such as empathy (Gallese, 2001; Cheng et al., 2008; Yang et al., 2009), theory of mind (Pineda and Hecht, 2009), speech perception (Moreno et al., 2013) and many other socio-cognitive processes (see Vanderwert et al., 2013 for a review). Furthermore, differences in mu rhythm response between clinical and typical samples have been used to suggest atypical MN response in conditions such as Autism Spectrum Disorder (Oberman et al., 2005, 2008; Bernier et al., 2007, 2013), schizophrenia (Singh et al., 2011; McCormick et al., 2012; Horan et al., 2014) and addiction (Pineda and Oberman, 2006).

There are, however, two important issues with the claim that mu rhythm indexes MN activity. First, most studies do not provide a convincing demonstration of the specificity of mu rhythm response. For the mu rhythm to be considered a valid index of MN, it should show

52 crossmodal action specificity, that is that the response associated with one action should be
53 similar whether it is observed or executed (crossmodality), but it should also be distinguishable
54 for different actions (specificity; Kilner and Lemon, 2013; Oosterhof et al., 2013). Without
55 demonstration of specificity, it is possible that the similarity of mu rhythm responses during
56 action observation and execution reflects general effects of task engagement, attention, readiness
57 to act or arousal-related activation involving non-mirror neuronal populations (Dinstein et al.,
58 2008; Cook et al., 2014). Second, empirical evidence suggests that the mu rhythm might index
59 sensory processing rather than motor activity (Cheyne et al., 2003; Ritter et al., 2009; Coll et al.,
60 2015). Thus, the mu rhythm may index the observation and receipt of tactile stimulation rather
61 than the observation and execution of actions.

62 Given that the mu rhythm is often used to assert the involvement of MN in a variety of
63 cognitive processes and clinical conditions, it is important to ensure its validity as an index of
64 MN activity by verifying that it shows crossmodal specificity to observed and executed actions.
65 Accordingly, we used crossmodal pattern classification to assess the specificity of the mu rhythm
66 during action observation and action execution. Furthermore, the degree of tactile stimulation
67 during action observation and execution was manipulated both by the application of a vibratory
68 tactile stimulation to the hand and by action transitivity (whether actions were, or were not,
69 object-directed - the former, but not the latter, generating cutaneous tactile stimulation). If the
70 mu rhythm represents MN activity, then crossmodal classification of two different types of
71 actions should be accurate at above-chance levels, and superior to the classification of tactile
72 stimulation. In contrast, if the mu rhythm indexes tactile mirroring, classification accuracy
73 should be above-chance when classifying the presence or absence of tactile stimulation, but at
74 chance for action type.

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Materials and methods

Experimental Design

The crossmodal specificity of the mu rhythm to two different actions (Action Type factor) was assessed while manipulating the amount of tactile stimulation involved in these actions in two different ways. The first manipulation related to the presence or absence of an external tactile stimulation (Vibration factor), and the second concerned whether the actions were directed towards an object or simply mimed (Transitivity factor). In order to assess the crossmodal specificity of the mu rhythm to action or stimulation type, and to maximise the number of trials that could be used for multivariate classification, we analysed the data using a fractional factorial design in which only the main effect of each condition was investigated. We therefore independently tested the effect of Action Type, Vibration and Transitivity while collapsing across the two other conditions. If the mu rhythm is specific to the action observed and executed, then the crossmodal classifier should be able to discriminate the two actions. If the mu rhythm is sensitive to differences in tactile stimulation, then the classifier should be able to discriminate between the presence and absence of the vibration and between transitive and intransitive actions. We predicted that crossmodal classification accuracy in central channels would increase with the strength of the difference in tactile stimulation in each condition and would thus follow a Vibration > Transitivity > Action Type pattern. We used three main approaches to test this crossmodal classification. First, to investigate the scalp distribution of the effects, we performed exploratory classification analyses on the time-frequency activity of the mu rhythm on each channel and its neighbours using a spatial searchlight approach (Kriegeskorte et al., 2006). Second, to visualise the neural sources contributing to the observed scalp effects, a spatial searchlight was also used on mu rhythm activity at the source level. Finally, to test the

108 claim that the central mu rhythm shows crossmodal specificity, region of interest (ROI) analyses
109 were performed using a crossmodal classifier in a central cluster of channels selected according
110 to the mu rhythm literature. To ensure that any crossmodal effect observed in this central cluster
111 is specific to the central alpha mu rhythm and not confounded with the occipital alpha rhythm
112 (Hobson and Bishop, 2016), these analyses were performed at both central and occipital scalp
113 locations. We predicted that crossmodal classification would be observed only at the central
114 location.

115 **Participants**

116 Twenty healthy right-handed adults (12 females) aged on average 24.60 years (SD =
117 6.75, range = 19-49) were recruited through university-wide advertisements and gave written
118 informed consent to take part in this study. Exclusion criteria included being over 50 years old or
119 any reported history of neurological or psychiatric disorder. The study was approved by King's
120 College London Psychiatry, Nursing and Midwifery Research Ethics Subcommittee and
121 participants received an honorarium for their participation.

122 **EEG recordings**

123 EEG activity was acquired from a 61 channel (extended 10-20 montage) DC-coupled
124 recording system (Brain Products, Munich, Germany, RRID:SCR_009443). Three additional
125 EOG electrodes were placed below the left eye and at 1 cm from the outer canthi. The sampling
126 rate was 500 Hz, with reference at FCz and ground at AFz. Impedances were maintained below
127 10 k Ω .

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121 Vibration stimulator

122 A custom-built stimulator was fixed on the back of the participant's right hand using
123 medical tape. This stimulator consisted of two round cell phone micro vibration motors (10 x 2.7
124 mm) vibrating at approximately 10 000 rotations per minute placed side by side on a piece of
125 thin cardboard and sealed with black electrical tape. When the stimulator was turned on, it
126 produced a continuous vibrating sensation on the back of the hand. A yellow LED light was
127 placed on the top of the motors and was lit when the stimulator was turned on. The stimulator
128 was wired into a USB relay switch and controlled by the stimuli presentation software (E-prime
129 2.0, Psychology Software Tools, Sharpsburg, PA, RRID:SCR:009567). The wire was fixed onto
130 the participant's forearm with medical tape to ensure that it did not interfere with action
131 execution during the experimental task. A second identical stimulator was placed near the
132 participant's arm and turned on during trials in which the hand stimulator remained off in order
133 to create a similar sound.

134 Visual stimuli

135 The visual stimuli consisted of 3000 ms video clips depicting a hand wearing the
136 vibration stimulator executing one of the 6 types of actions varying according to Action Type
137 (Precision grip, Whole-hand grip), Vibration (Vibration On, Vibration Off) and Transitivity
138 (Transitive, Intransitive) filmed from a first-person point of view (Figure 1). During the
139 Transitive trials, the hand was seen executing one of two actions on an empty plastic bottle
140 placed on a black table. For the Intransitive trials, the bottle was absent from the screen and the
141 same actions were mimed without the bottle. For Precision Grip trials, the hand started flat on the
142 table at the right of the screen, picked up (or mimed picking up) the bottle using a thumb and
143 index grip on the cap of the bottle and raised it approximately 15 cm before placing it back on

144 the table. For the Whole-hand Grip trials, the hand picked up (or mimed picking up) the bottle
145 using a whole-hand grip on the body of the bottle. During Vibration On trials, the stimulator was
146 turned on, and this was visible due to the vibration of the stimulator and the yellow LED light.
147 During Vibration Off actions the stimulator was not turned on. All video clips were presented
148 without sound. Two models (one female) were recorded while executing the actions to the beats
149 of a metronome to ensure similar timing during all video clips. The models executed the actions
150 twice for a total of 32 different stimuli (8 types x 2 models x 2 executions). The video clips were
151 presented on a 17-inch monitor located at approximately 60 cm from the participant using the E-
152 Prime 2.0 software (Psychology Software Tools, Sharpsburg, PA, RRID:SCR:009567).

153 ----- Figure 1 about here -----

154 **Procedure**

155 Participants sat in a dimly lit room. After giving informed consent, the EEG cap and the
156 stimulator were installed and participants received verbatim instructions for the task. During the
157 experimental task, participants were asked to either observe the video clips or to execute one of
158 the six action types using the same plastic bottle as in the video clips. To ensure that the bottle
159 did not fall during the experiment it was stabilised using a square piece of cardboard fixed at its
160 base. A practice session was carried out during which each of the 6 action types was first
161 observed in a video clip and then executed by the participants using the plastic bottle. During this
162 practice session, participants experienced the vibro-tactile stimulation and observed the lighting
163 of the LED. They were explicitly instructed that the hand in the video clips wore the same
164 vibration stimulator, and that this hand received the same vibrating stimulation when the LED
165 light was turned on. The practice session was repeated if necessary to ensure that all participants
166 understood the instructions and executed the actions in a correct manner with appropriate timing.

167 After the practice session, an occlusion box was placed over the participant's arm to
168 prevent the participant from observing his or her actions and the LED light during the
169 experiment. Movements were monitored using a webcam placed inside this box and trials with
170 incorrect action execution or with movement during observation were noted and removed from
171 the analyses. All experimental conditions were blocked within mini-blocks of ten trials during
172 which participants either executed or observed the same action type ten times. During Execution
173 blocks, participants first saw the instructions indicating which action type should be executed
174 (e.g. "Execute, Fine *OR* Full Grip, With *OR* Without the object, With *OR* Without vibration) for
175 5000 ms followed by ten trials consisting of an 800 ms green fixation cross, a 1000-5000 ms
176 jittered white fixation cross and a 3000 ms green circle. Participants were instructed to blink
177 during the instructions and the green fixation cross but to refrain from blinking for the rest of the
178 task. Participants were told to begin executing the action as soon as they saw the green circle and
179 to have their hand back on the table before the green circle disappeared. During Vibration On
180 trials, the vibration stimulator was turned on during the presentation of the green circle. During
181 Vibration Off trials, a second stimulator was turned on in order to produce a similar sound.

182 During Observation blocks, participants received the instruction "Please remain still and
183 watch the video clips" followed by ten trials consisting of the green and white fixation crosses
184 presented for the same duration as the Execution blocks and a video clip. The stimulator was
185 never turned on during the Observation blocks. Eight out of the 28 Observation blocks were
186 catch blocks during which one of the ten video clips was presented with a red dot in the centre.
187 At the end of all Observation blocks, participants saw a prompt asking them to indicate whether
188 they saw a red dot in one of the video clips using their left hand placed on a keyboard. Catch
189 blocks were not included in the EEG analyses. Finally, during Baseline blocks, participants were

190 instructed to remain still and to wait for the next instruction and then observed a black screen for
191 21 s.

192 Participants performed 32 execution or observation blocks of ten trials, two for each of
193 the eight experimental condition [Vibration (On, Off) x Transitivity (Object, No Object) x
194 Action Type (Precision, Whole-hand)]. This resulted in 160 observation and 160 execution trials
195 that were used for analyses. Eight catch trial blocks were used to ensure continuous attention to
196 the stimuli and were not included in the EEG analyses. Participants performed four experimental
197 sessions in which four execution, four observation and two catch blocks were presented in a
198 random order. Three baseline blocks were presented at the beginning, middle and end of the
199 session. The duration of the task was approximately 60 minutes and participants were
200 encouraged to take breaks between each session.

201 **Statistical Analyses**

202 All EEG analyses were performed with the FieldTrip (Oostenveld et al., 2011,
203 RRID:SCR_004849) and CosMoMvpa (Oosterhof et al., 2016, RRID:SCR_014519) toolboxes
204 within Matlab 2016a (The Mathworks Inc, Natick, MA, RRID:SCR_001622). The analyses
205 workflow for both univariate and multivariate analyses is detailed in Figure 2. While the
206 crossmodal specificity of the alpha band (8-13 Hz) was the main focus of this study, all analyses
207 were also performed in the beta band (15-25 Hz) for completeness and in line with previous
208 suggestions of a link between beta rhythm suppression and MN activity (e.g. Rossi et al., 2002).

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213 Catch trial accuracy

214 Responses to the prompts presented after each observation blocks were scored as 0 (miss
215 or false alarm) or 1 (correct detection or correct rejection) and averaged in order to obtain a catch
216 trial accuracy score for each participant.

217 EEG preprocessing

218 EEG data were first bandpass filtered between 1 and 50 Hz and an additional 50 Hz notch
219 filter was used to reduce electrical noise. The data were then epoched -1000 to 3500 ms relative
220 to the onset of the video clips or the execution cue. Epochs of the same length were also taken
221 from the baseline periods. This led to a total of 160 observation and 160 execution trials.

222 Independent component analyses were used to remove from the signal components that were
223 associated with eye blinks, movements or other obvious artefacts. The data were then visually
224 inspected and channels that were consistently bad throughout the experiment or trials with
225 artefacts were removed from the analyses. Additionally, trials for which the participant
226 performed the incorrect action or moved when they were not supposed to move were removed
227 from the analyses. These procedures led to the removal of an average of 4.81% (SD =3.68, range
228 = 2-15 %) of trials. After epoch rejection, removed channels were interpolated using the average
229 activity of neighbouring channels.

230 For analyses at the channel level, the time-frequency representation of the data was
231 obtained by applying a Fourier transformation in Hanning-tapered sliding time windows with a
232 fixed length of 500 ms and moving in steps of 50 ms. Power was calculated from 5 to 30 Hz in
233 steps of 1 Hz.

234 For analyses at the source level, sources were identified using Dynamic Imaging of
235 Coherent Sources (DICS; Gross et al., 2001), a frequency domain beamforming technique.

236 Activity was source localised in a 250 to 2750 ms time window. A frequency of 10 Hz with a
237 smoothing window of +/- 2 Hz was used for the alpha band and a frequency of 20 Hz with a
238 smoothing window of +/- 5 Hz was used for the beta band. These time and frequency windows
239 were selected following visual inspection of the univariate effects on the basis of those time and
240 frequency windows which included the majority of the alpha and beta suppression. In brief, a
241 volume conductor model was built for all participants using the boundary element method and a
242 standard MNI template. A 10 mm-spaced dipole grid was wrapped onto the MNI brain template
243 and a normalised lead field was calculated. DICS was performed for each trial using a common
244 spatial filter computed from the combination of all trials and a 5% lambda regularisation
245 parameter. This resulted in the estimation of the alpha activity at each grid point for each
246 participant and trial.

247 **EEG analyses**

248 **Univariate analyses:** In order to compare the mu rhythm suppression in the current
249 experiment to that obtained in previous studies, we first analysed our data using traditional
250 univariate analyses. For these analyses, the average power in each condition was normalised
251 relative to a -500 to 0 ms pre-stimulus baseline. Power was then averaged across frequency
252 (alpha: 8-13 Hz, beta: 15-25 Hz) and time (0-3000 ms).

253 Exploratory analyses were first performed to investigate the scalp distribution of the main
254 effect of each condition within each modality. To this end, a two-tailed paired sample t-test
255 comparing the two levels of each condition was performed at each channel. The significance of
256 this test was assessed using a nonparametric permutation approach in which this test was
257 performed 10 000 times on the same data with randomly permuted condition labels. P-values
258 were obtained by taking the proportion of random tests with a test statistic equal or superior to

259 the original value and were corrected for multiple comparisons using cluster-based correction.
 260 Channel clusters were determined by including each channel's immediate neighbours using
 261 triangulation (on average 6.7 neighbours) and cluster statistics were obtained by summing the t-
 262 scores of neighbouring channels exceeding the critical value ($p < 0.05$; see Maris and Oostenveld
 263 (2007) for the detailed procedure).

264 ROI analyses were performed to compare the observed effects to previous studies
 265 investigating the alpha mu rhythm suppression during action observation and execution. In line
 266 with these previous studies, ten central channels (C1-2-3-4-z, CP1-2-3-4-z) were selected for
 267 further analyses. An equivalent number of occipital channels (PO3-4-7-8-9-10-z, O1-2-z) were
 268 selected to serve as the control occipital site where no cross-modal effects were expected. The
 269 main effect of each experimental condition was calculated by taking the difference between the
 270 two levels of each of the conditions (Transitive-Intransitive, Vibration On-Vibration Off, Whole-
 271 hand grip-Precision grip). These differences were entered into a three-way repeated-measures
 272 ANOVA to investigate the effects of Modality (Execution, Observation), Location (Central,
 273 Occipital) and Condition (Transitivity, Vibration and Action).

274 -----
 275 ----- Figure 2 about here -----

276
 277 **Multivariate pattern classification:** A linear support vector machine classifier was used
 278 to perform a five-fold cross-validated classification on all trials. Subsets of trials were created for
 279 classifier input by dividing the data into five independent chunks for each modality (for a total of
 280 ten chunks) which were balanced to ensure an equal number of trials for each condition tested. A
 281 leave-one-chunk-out cross-validation was performed in which four chunks were used to train the
 282 classifier, which was then tested on an independent chunk. For each participant and

283 classification, activity within each trial was normalised across all trials in the training set using a
284 z-score transformation and the same normalisation parameters were used to normalise trials of
285 the testing set. Note that for each classification, all trials in one modality were included since all
286 trials belonged to one of the two levels of each experimental condition. With this approach, at
287 least 135 trials were used for classification (Mean = 152.36, SD = 6.32 range 135-160)
288 depending on the number of trials left after artefact rejection. There was no significant difference
289 in the number of trials included in each condition as confirmed with a 2 (Execution, Observation)
290 x 3 Condition (Vibration, Action Type, Transitivity) repeated measures ANOVA performed on
291 the number of trials left after artefact rejection (all p s > 0.60).

292 Classification was first performed within modality (unimodal classification), to ensure
293 that the mu rhythm response for each condition was distinguishable within modality. For the
294 unimodal classification analysis, the classifier was trained and tested on trials of the same
295 modality (Execution or Observation). Then, for the crossmodal classification analysis, the
296 classifier was trained on four chunks from one modality and tested on a chunk of trials of the
297 opposite modality. This procedure was repeated five times for each modality, condition and
298 location. The mean crossmodal classification accuracies for each modality as well as Friedman
299 tests carried out on the classification accuracies in the clusters of interest suggested a similar
300 pattern of results for both modalities. The accuracies obtained were thus averaged across
301 modalities to obtain one classification accuracy for each participant, condition and location for
302 both unimodal and crossmodal classifications.

303 At the channel level, the classifier was trained to use the three dimensions of the data,
304 that is time (0-3 s in bins of 50 ms; 61 time bins), frequency (8-13 Hz or 15-25 Hz, in bins of 1
305 Hz; 6 or 11 frequency bins) and location (on average 6.7 channels in the neighbourhood structure

306 for searchlights or 10 channels in the clusters of interest for regions of interest analysis), to
307 discriminate between the two levels of each main effect (Transitive vs Intransitive, Precision grip
308 vs Whole-hand Grip, Vibration on vs Vibration off). For the whole-scalp spatial searchlight
309 analysis, the same neighbourhood structure as used in the univariate analysis was used.
310 Classification was thus performed at each channel using all time-frequency information from this
311 channel and its neighbours (on average 6.7 neighbours; see Tucciarelli et al., 2015; Turella et al.,
312 2016 for a similar approach but in time-frequency-sensor space using MEG). This resulted in
313 classification accuracy maps showing classification accuracy at each channel for each condition
314 and participant. Maps in each condition were submitted to a one-sample t-test against chance
315 accuracy (50%) at the group level and the significance of this test was assessed using the same
316 permutation procedure used for univariate whole-scalp analysis (see section Univariate
317 analyses). For the ROI analyses at the channel level, the same time-frequency dimensions were
318 used, but the classifier was applied separately on two clusters of ten central channels and ten
319 occipital channels of interest. Classification accuracy in each condition and location was
320 compared against chance using a Wilcoxon signed rank test contrasting classification
321 performance with chance accuracy of 0.5 (Carlson et al., 2013; Ritchie et al., 2015). The main
322 effect of Condition (Vibration, Action Type, Transitivity) was assessed separately at the central
323 and occipital channels using the Friedman test of differences.

324 At the source level, the classifier was trained to discriminate between the two levels of
325 each main condition by using the spatial pattern of source activity. A spatial searchlight approach
326 was used by building a neighbourhood structure using all grid points within a sphere with a
327 radius of 2 cm from each grid point (on average 28.6 neighbours). Classification was then
328 performed at each grid point and its neighbours. Classification accuracies in source space were

329 projected to a standard MNI template for visualisation. Source accuracy maps in each condition
 330 were submitted to a one-sample t-test against chance accuracy (50%) at the group level and the
 331 significance of this test was assessed using the same permutation procedure used for univariate
 332 whole-scalp analysis (see section Univariate analyses).

333 **Results**

334 **Catch trials accuracy**

335 The average detection accuracy was 97.40 % (SD = 3.18%, range = 91-100%) indicating
 336 that participants correctly identified the presence of the catch trial cue on the majority of
 337 presentations.

338 **Univariate analyses**

339 Scalp distribution of the mu rhythm suppression in the alpha band as well as a time-
 340 frequency representation of this suppression in each cluster of interest are shown in Figure 3. The
 341 whole-scalp analyses of the alpha mu rhythm suppression performed in the observation modality
 342 revealed significant main effects of Transitivity at a central left cluster of channels indicating
 343 stronger mu suppression for the observation of transitive movements relative to the observation
 344 of intransitive movements. No significant main effects of Vibration and Action Type were found
 345 during observation. The same analyses performed in the execution modality showed significant
 346 main effects of Vibration and Transitivity. These effects indicated significantly stronger
 347 suppression for ‘vibration on’ trials relative to ‘vibration off’ trials in a large frontal-right cluster
 348 of channels as well as significantly stronger suppression for executed intransitive trials relative to
 349 transitive trials in a cluster of left central and parieto-occipital channels. No significant main
 350 effect of Action Type was found during execution.

351 -----Figure 3 and 4 about here -----

352 Mu rhythm suppression at each level of the three main experimental conditions at the
353 central and occipital clusters of interest are shown in Figure 5A. The three-way repeated
354 measures ANOVA revealed a significant Modality x Location interaction [$F(1, 19) = 5.03, p =$
355 $0.037, \eta_p^2 = 0.21$] indicating that the overall effect of the experimental conditions was stronger at
356 the central relative to the occipital location in the observation modality but not in the execution
357 modality. There was also a significant Modality x Type interaction [$F(2, 38) = 5.70, p = 0.012,$
358 $\eta_p^2 = 0.23$] due to the fact that in the Transitive condition, transitive trials led to a stronger mu
359 suppression relative to intransitive trials during observation, but the opposite effect was present
360 during execution. There was no significant main effects of Modality, Location or Type and no
361 other interaction reached significance (all $ps > 0.05$).

362 Scalp distribution of the mu-rhythm suppression in the beta band as well as a time-
363 frequency representation of this suppression in each cluster of interest are shown in Figure 4. The
364 whole-scalp analyses of the beta rhythm suppression performed in the observation modality
365 revealed significant main effects of Vibration in a large cluster of channels over the posterior left
366 hemisphere, indicating stronger beta suppression for the observation of movements with a
367 concurrent vibration compared to the observation of movements without concurrent vibration.
368 The same analyses performed in the execution modality did not show any univariate difference
369 between the conditions.

370 Mu-rhythm suppression in the beta band at each level of the three main experimental
371 conditions at the central and occipital clusters of interest are shown in Figure 5B. The three-way
372 repeated measures ANOVA revealed a significant Modality x Location interaction [$F(1, 19) =$
373 $5.78, p = 0.027, \eta_p^2 = 0.23$] indicating that the overall effect of the experimental conditions on
374 beta suppression was stronger for the execution modality relative to observation at the central

375 location, while the opposite effect of modality was observed at the occipital location. There was
376 no significant main effects of Modality, Location or Type and no other interaction reached
377 significance (all $ps > 0.05$).

378 ----- Figure 5 about here -----

379

380 **Multivariate pattern classification**

381 **Unimodal classification:** As shown in Figure 5A, the spatial searchlight analysis
382 performed at the channel level revealed widespread above-chance unimodal classification
383 accuracy across all channels for the three experimental conditions in both the alpha and beta
384 band. As shown in Figure 5B, classification at the source level for the alpha band suggested that
385 widespread sources mainly located in the frontal and parietal areas were responsible for the
386 unimodal classification in all three conditions. Permutation analyses indicated that all these
387 sources showed significantly above chance classification. This was reflected in the ROI analyses
388 in which Wilcoxon signed-rank tests revealed significantly above-chance classification accuracy
389 for all conditions at both the central and occipital electrode clusters (see Figure 6C for p -values).
390 Friedman tests indicated that there was a significant effect of Condition at the central cluster
391 [$\chi^2(2) = 6.40, p = 0.041$] due to a significantly higher unimodal classification accuracy in the
392 Transitivity compared to the Action Type manipulation ($p = 0.037$). There was no significant
393 effect of Condition at the occipital cluster [$\chi^2(2) = 2.45, p = 0.293$]. For the beta band, sources
394 mainly located in the frontal and temporal areas showed significantly above chance classification
395 and were responsible for the unimodal classification in all three conditions. ROI analyses using
396 Wilcoxon signed-rank tests revealed significantly above-chance classification accuracy for all
397 conditions at both the central and occipital electrode clusters (see Figure 6C for p -values).

398 Friedman tests indicated that there was no significant effect of Condition at the central [$\chi^2(2) =$
399 1.80, $p = 0.091$] or occipital cluster [$\chi^2(2) = 1.30$, $p = 0.522$].

400

401 ----- Figure 5 about here -----

402

403 **Crossmodal classification:** For the alpha band, the spatial searchlight analysis
404 performed at the channel level revealed clusters of channels showing above-chance crossmodal
405 classification accuracy for the three experimental conditions (Figure 7A). For the Vibration
406 condition, this cluster covered mainly central channels, for the Transitivity the significant cluster
407 covered left central and temporal channels while a cluster of left parieto-occipital channels
408 showed above-chance classification in the Action Type condition. The crossmodal classification
409 accuracy at the source level is shown in Figure 7B for visualisation purposes – it should be noted
410 that the permutation analyses indicated that classification was not significantly above chance at
411 the source level. Regardless of significance, source level analyses suggested that for the
412 Vibration condition a right parietal cluster partly covering the somatosensory cortex contributed
413 most to the crossmodal classification. In the Transitivity condition, sources generating the
414 crossmodal classification were widely distributed mainly over fronto-parietal areas. Finally, for
415 the Action Type condition, small clusters located over temporal and occipital areas showed
416 above-chance cross-modal classification. As shown in Figure 7C, the ROI analyses revealed that
417 significantly above-chance crossmodal classification accuracy was reached only in the Vibration
418 and Transitivity conditions and only at the central cluster. This was confirmed by Friedman tests
419 showing a significant main effect of Condition at the central cluster [$\chi^2(2) = 9.10$, $p = 0.011$] but
420 not at the occipital cluster [$\chi^2(2) = 0.90$, $p = 0.638$]. At the central cluster, this effect was due to

421 significantly higher classification in the Vibration condition compared to the Action Type
422 condition ($p = 0.025$) while there was no other pairwise difference between the conditions (all ps
423 > 0.18).

424 The crossmodal classification performed in the beta band did not indicate any
425 significantly above-chance classification in the searchlight analysis performed at the channel
426 level (Figure 7A), at the source level (Figure 7B) or in the ROI analyses (Figure 7C).

427 -----
428 ----- Figure 7 about here -----
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Discussion

431 The present study examined the validity of the claim that the EEG mu rhythm is a valid
432 index of MN activity by testing for the presence of crossmodal specificity in response to
433 observed and executed actions. Moreover, it assessed the alternative prediction that the mu
434 rhythm demonstrates crossmodal and specific responses to the observation and receipt of tactile
435 stimulation. This was achieved using a multivariate crossmodal classification approach to test
436 whether the central mu rhythm contains sufficient crossmodal information to discriminate
437 between two different types of actions, between the presence or absence of tactile stimulation,
438 and between transitive and intransitive actions.

439 Results from the crossmodal classification of mu rhythm response at the channel level
440 were as predicted by the tactile stimulation account, and support the idea that the central mu
441 rhythm shows crossmodal specificity primarily for the somatosensory features of observed and
442 executed action. While exploratory searchlight analyses indicated significant crossmodal
443 classification for all conditions, central channels contributed mostly to the classification of

444 conditions showing strong variation in tactile features. Crossmodal classification of action type
445 was achieved for alpha-band activity that is not central, and not likely to be reflective of mirror
446 neuron system activity. Mu suppression experiments investigating mirror neuron processes
447 commonly consider changes in activity at the central sites to be reflective of mirror neuron
448 system activity. The results from the ROI analyses in the current study strongly suggest that
449 responsivity at these sites is not in keeping with mirror neuron accounts of central mu
450 suppression. This was supported by a priori region of interest analyses performed at a cluster of
451 central channels which revealed above-chance crossmodal classification only for the tactile
452 stimulation and transitivity conditions, and significantly higher classification accuracy for the
453 presence of tactile stimulation relative to the type of action. The same analysis performed at the
454 control occipital channels did not indicate any significant classification. The crossmodal
455 specificity of the mu rhythm to somatosensory features of actions suggests that the central mu
456 rhythm response to action observation and execution observed in the current and previous studies
457 might be better explained by sensory processing rather than motor mirroring (Dinstein et al.,
458 2008; Cook et al., 2014; Coll et al., 2015). It should be noted however, that the preceding studies
459 reported the results of univariate analyses, rather than multivariate analyses.

460 While this is, as far as we are aware, the first study to investigate the crossmodal
461 specificity of mu rhythm responses using multivariate classification, it is not the first to suggest
462 that the crossmodal mu rhythm response indexes somatosensory features of action rather than
463 action type (Coll et al., 2015). The association of the mu rhythm with sensory processing has
464 also been demonstrated by several previous studies. The central alpha mu rhythm is known to be
465 modulated by somatosensory attention (Jones et al., 2010; Anderson and Ding, 2011), and pre-
466 stimulation mu rhythm activity can reliably predict the detection of a somatosensory stimulus

467 (Linkenkaer-Hansen and Nikulin, 2004). Previous studies using fMRI or source localisation also
468 indicate that the mu rhythm can be associated with the activity of the somatosensory cortices
469 (Hari et al., 1998; Cheyne et al., 2003; Ritter et al., 2009; Arnstein et al., 2011) and is responsive
470 to the observation of tactile stimulation (Muthukumaraswamy and Johnson, 2004; Coll et al.,
471 2015). In line with this previous research, we found above-chance crossmodal classification
472 accuracy when the classifier was used to discriminate between the presence or absence of tactile
473 stimulation in the self or in the other in central channels, and this accuracy was significantly
474 higher than for classification of action types. The source analyses performed in the current
475 experiment did not reveal any significantly above-chance crossmodal classification at the source
476 level. This should be interpreted with caution given that the relatively sparse EEG montage used
477 and the lack of individual anatomical information make these statistical analyses highly
478 conservative. The visualisation of crossmodal classification accuracy at the source level
479 nevertheless suggests that crossmodal classification of the mu rhythm response to tactile
480 stimulation and transitivity was driven by fronto-parietal sources including somatosensory areas.

481 The unimodal classification results obtained in the current study suggest that the
482 unimodal mu rhythm response shows little specificity. Indeed, classifiers trained and tested on
483 trials of the same modality showed widespread above-chance classification at both channel and
484 source levels. Indirect evidence for the lack of spatial and functional specificity of the mu rhythm
485 response is also present in a recent meta-analysis of mu rhythm suppression studies. Fox and
486 collaborators analysed 85 studies and found that, across these studies, mu rhythm suppression
487 did not show many of the properties of MN activity, such as preference for object-directed
488 movement or biological motion. In addition, the effect size of alpha suppression compared to
489 baseline during action observation was not found to be greater at central electrodes compared to

490 occipital electrodes, suggesting that the contribution of the occipital alpha rhythm might explain
491 many of the effects reported in the literature (Fox et al., 2015; Hobson and Bishop, 2016).

492 To compare the results obtained from the multivariate pattern classification to the results
493 obtained in previous studies, we also performed a univariate analysis of mu rhythm suppression
494 relative to baseline for the same experimental conditions by averaging activity over all time-
495 frequency bins. When comparing the average mu rhythm suppression relative to baseline, we
496 found similar suppression effects in terms of effect size and location compared to previous
497 studies (see Fox et al., 2015 for a meta-analysis). However, this analysis showed that alpha
498 rhythm suppression was not specific to the central electrodes and was relatively insensitive to
499 differences between conditions. These results suggest that the analytical approach used in
500 previous research is inadequate to detect the specificity of crossmodal mu rhythm responses and
501 is insensitive to subtle differences between conditions. This was to be expected considering that,
502 by averaging over all features of the data, this approach does not take into account differences in
503 multivariate patterns that can differ between conditions and participants. This is also in line with
504 a recent high-powered preregistered report indicating that mu rhythm suppression effects found
505 using this analytical approach are weak and unreliable (Hobson and Bishop, 2016).

506 While not the primary focus of the study, activity in the beta band was submitted to the
507 same analyses as the alpha mu rhythm. Beta activity has also been previously associated with
508 MN activity although less frequently than the alpha mu rhythm (Muthukumaraswamy and Singh,
509 2008; Rossi et al., 2002). Here, beta activity was shown to contain unimodal information on the
510 different experimental conditions. This is in line with previous studies using a similar analytical
511 approach showing that beta activity can be used to classify observed (Tucciarelli et al., 2015) or
512 executed actions (Turella et al., 2016). However, the crossmodal classification of beta activity

513 was at chance level in all conditions. The current results therefore suggest that beta rhythm
514 suppression during action observation and action execution does not show crossmodal action
515 specificity.

516 Limitations to this study need to be acknowledged. First, it should be noted that the
517 crossmodal classification approach used in the current study could be quite conservative, and that
518 it might therefore lack the sensitivity to detect central crossmodal mu rhythm responses to the
519 motor features of the observed actions. It should also be noted that EEG activity represents a
520 superposition of the activity of large neuronal populations and channel level analyses might lack
521 the spatial specificity to demonstrate crossmodal classification of weaker effects. Therefore, even
522 though crossmodal classification at the central channels was clearly higher for sensory features
523 of actions, the absence of crossmodal classification for action types cannot be interpreted as the
524 absence of crossmodal specificity for observed and executed actions in the mu rhythm response.

525 In conclusion, we have shown that the central alpha mu rhythm shows crossmodal
526 specificity primarily for the observation and receipt of a tactile stimulation and that multivariate
527 pattern classification is more sensitive to subtle differences between conditions than univariate
528 analyses. This is to our knowledge the first study to use multivariate pattern classification to
529 assess the crossmodal specificity of EEG responses. Combined with other sources of evidence,
530 they question the appropriateness of mu rhythm suppression as a measure of MN activity and
531 suggest that multivariate crossmodal analyses are needed to adequately study this relationship in
532 the future. This study, and others, support the idea that a new framework is needed to explain the
533 significance of the central mu rhythm for social perception in health and in disease, and that the
534 search for this new framework should be directed away from a simplistic matching between mu

535 rhythm suppression and MN activity and employ methodologies that are able to take into account
536 the multivariate nature of EEG data.

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Legends

639 **Figure 1.** Frames from the visual stimuli illustrating the different types of action observed or
640 executed by the participants. Participants either performed a Transitive (right column) or an
641 Intransitive (left column) Whole-hand grip (top row) or Precision grip (bottom row). These
642 actions were observed and performed with the Vibration device on (bottom row) or the Vibration
643 device off (top row).

644 **Figure 2.** Schematic illustration of the analysis workflow for the univariate analyses (green
645 borders) and the multivariate analyses (blue borders) performed at the channel and source levels.
646 White boxes indicate analyses performed at the subject level while grayed out boxes indicate
647 analyses performed at the group level.

648 **Figure 3.** Scalp distribution of the alpha mu rhythm suppression relative to baseline for the two
649 levels of each Condition (A- Vibration, B-Transitivity, C-Action type) as a function of Modality
650 (Execution; Left; Observation; Right). The difference maps show clusters of channels with
651 significant main effects surviving correction for multiple comparisons for each Condition and
652 Modality. Time-frequency plots show the time course of frequency activity at the central and
653 occipital clusters of interest. Channels included in these clusters are marked on the scalp maps.

654 **Figure 4.** Scalp distribution of the beta suppression relative to baseline for the two levels of each
655 Condition (A- Vibration, B-Transitivity, C-Action type) as a function of Modality (Execution;
656 Left; Observation; Right). The difference map show clusters of channels with significant main
657 effects surviving correction for multiple comparisons for each Condition and Modality. Time-
658 frequency plots show the time course of frequency activity at the central and occipital clusters of
659 interest. Channels included in these clusters are marked on the scalp maps.

660 **Figure 5.** Mean (A) alpha and (B) beta suppression relative to baseline for the two levels of each
661 Condition (Vibration, Transitivity, Action type) as a function of Modality (Execution; Left,
662 Observation; Right) and Location (Central; left column, Occipital; right column). Error bars 95
663 % confidence interval and the black dots show the mean suppression for each subject.

664 **Figure 6.** Results for the multivariate unimodal classification for the alpha (top) and beta
665 (bottom) bands. (A) Results from the searchlight analyses at the channel level and maps showing
666 cluster of channels with classification accuracy significantly above-chance (0.50) and surviving
667 correction for multiple comparisons. (B) Classification accuracy for the searchlight analyses
668 performed at the source level. Only grid points with accuracy above the 95% of the maximum
669 accuracy were projected to the scalp for visualisation purposes. All grid points projected show
670 significantly above-chance accuracy. (C) Mean and distribution of classification accuracy as a
671 function of Condition and Location for the classification performed in the central and occipital
672 clusters of interest. The dotted line illustrates chance classification accuracy (0.5), the error bars
673 show the 95% confidence interval and the black dots show the mean classification accuracy for
674 each participant.

675 **Figure 7.** Results for the multivariate unimodal classification for the alpha (top) and beta
676 (bottom) bands. (A) Results from the searchlight analyses at the channel level and maps showing
677 clusters of channels with classification accuracy significantly above-chance (0.50) and surviving
678 correction for multiple comparisons. (B) Classification accuracy for the searchlight analyses
679 performed at the source level. Only grid points with accuracy above the 95% of the maximum
680 accuracy were projected to the scalp for visualisation purposes. Crossmodal classification at the
681 source level is illustrated for visualisation purposes only as no grid points projected showed
682 significantly above-chance accuracy. (C) Mean and distribution of classification accuracy as a
683 function of Condition and Location for the classification performed in the central and occipital
684 clusters of interest. The dotted line illustrates chance classification accuracy (0.5), the error bars
685 show the 95% confidence interval and the black dots show the mean classification accuracy for
686 each participant.

Intransitive

Transitive

Whole-hand
grip



Precision
grip



Analysis workflow

Data preprocessing

Univariate analyses

Time-frequency decomposition

Baseline normalisation (-500 to 0 ms)

Average power across the 0-3 s trial duration and the 8-13 or 15-21 Hz frequency band at each channel

Region of interest analyses:
Average activity across channels in the central or the occipital cluster to obtain one power change value for each for cluster, condition level and participant.

3 Condition x 2 Location x 2 Modality repeated measures ANOVA on main effect of each condition. Figure 4

Paired t-test comparing the main effect of condition at each channel. Significance assessed with permutations and a cluster-based correction for multiple comparisons. Figure 5.

Region of interest analyses:
Train the classifier to discriminate between the two levels of each condition using time-frequency information (0-3 s; 8-13 Hz) in both the central and occipital channels. Cluster of interest to obtain one unimodal and one crossmodal classification accuracy for each cluster, condition and participant.

Wilcoxon signed ranked test against chance accuracy for each condition and location. Friedman tests for the effect of Condition on classification accuracy at each location. Figure 5C and 6C.

Multivariate analyses

Channel level

Source level

Time-frequency decomposition

Frequency domain beamforming

Define a neighbourhood structure by taking the neighbours of each channel using triangulation.

Define a neighbourhood structure by taking all grid points located in a 2 cm spherical radius of each grid point.

Cross-validation partitioning:
Partition trials into five independent "chunks" of trials

Channel level searchlight:
For each channel: train a multivariate classifier on 4/5 chunks of trials to discriminate between the two levels of each condition using time-frequency information (0-3 s; 8-13 Hz) in the current channel and its neighbours. Test the classifier on the trials in the remaining chunk. Repeat for each chunk and each modality.

Source level searchlight:
For each grid point: train a multivariate classifier on 4/5 chunks of trials to discriminate between the two levels of each condition using the spatial pattern of source activity in each 2 cm sphere. Test the classifier on the trials in the remaining chunk. Repeat for each chunk and each modality.

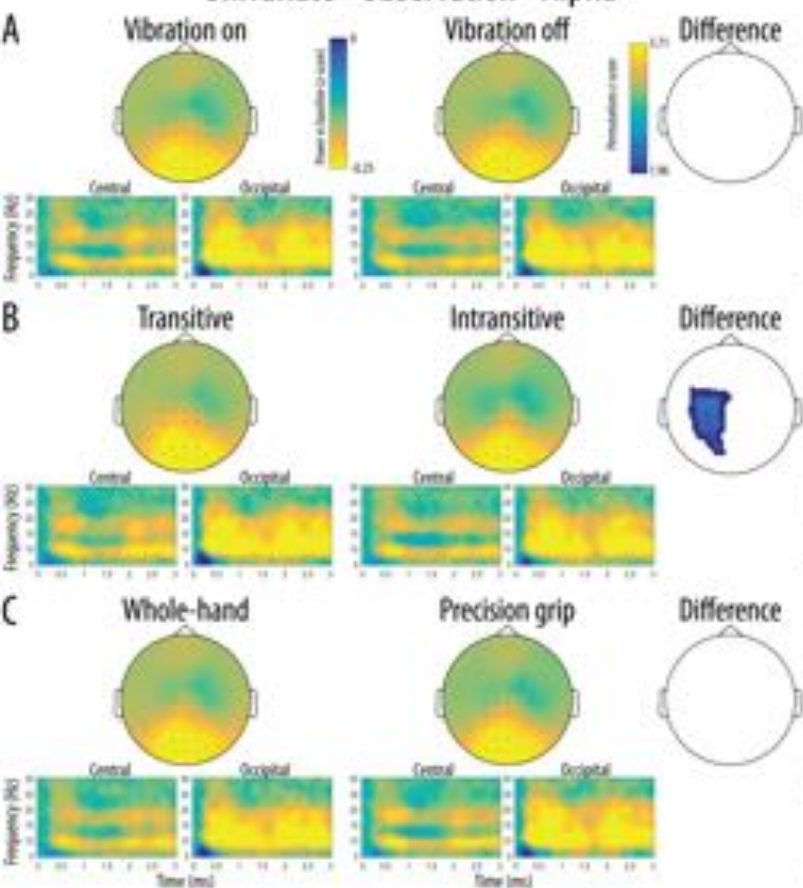
Unimodal: Train on trials in one modality and test on trials from the same modality.
Crossmodal: Train on trials in one modality and test on trials from the other modality.

Average searchlights across cross-validation folds and modalities to obtain one unimodal and one crossmodal classification accuracy map for each condition and participant.

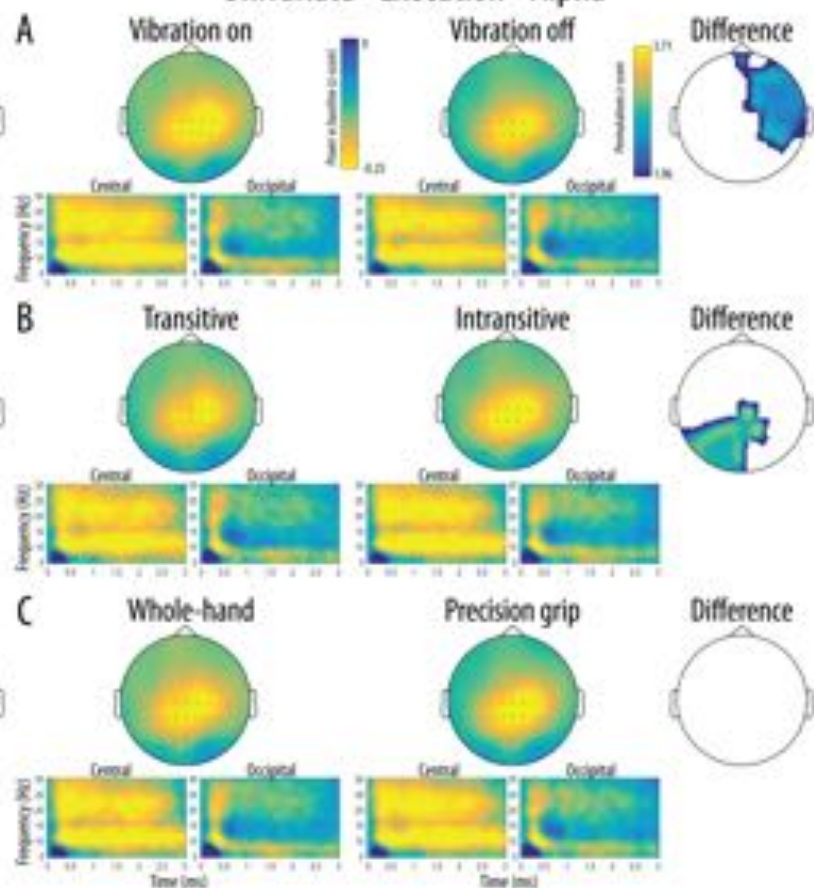
One-sample t-test against chance classification accuracy at each channel. Significance assessed with permutations and a cluster-based correction for multiple comparisons. Figure 5a and 6A.

Projection of source classification accuracy to a standard brain template. Figure 5B and 6B.

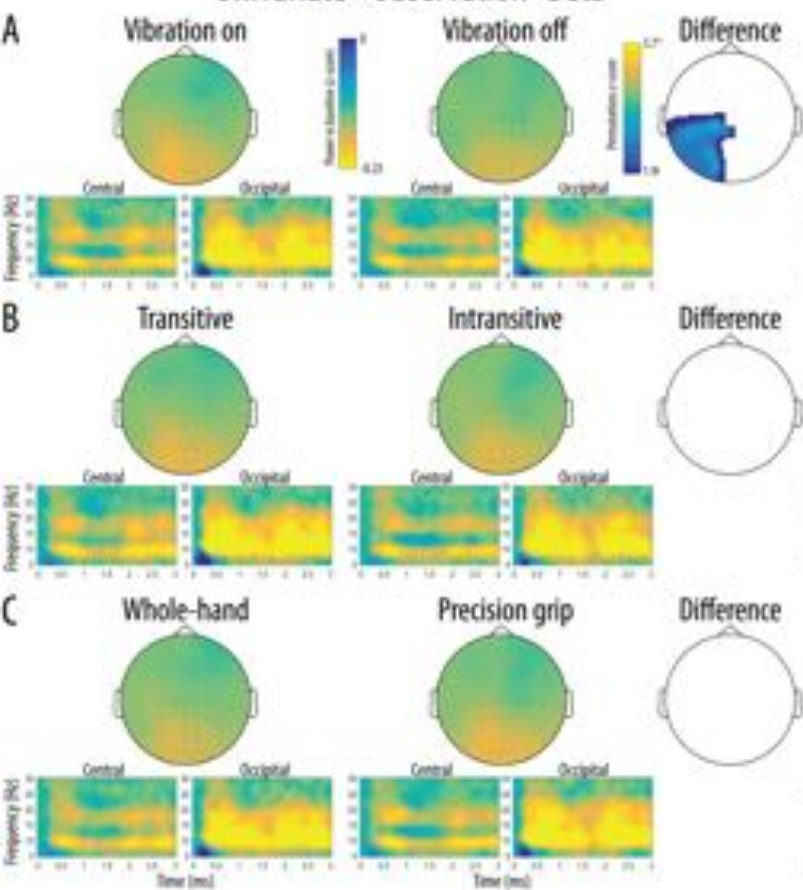
Univariate - Observation - Alpha



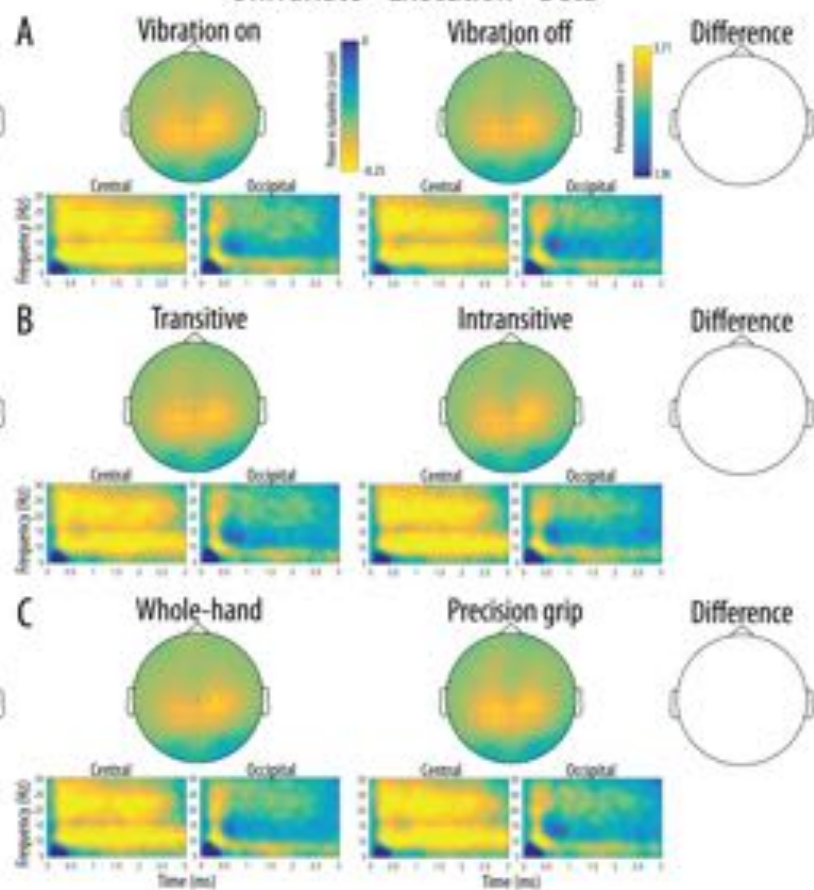
Univariate - Execution - Alpha

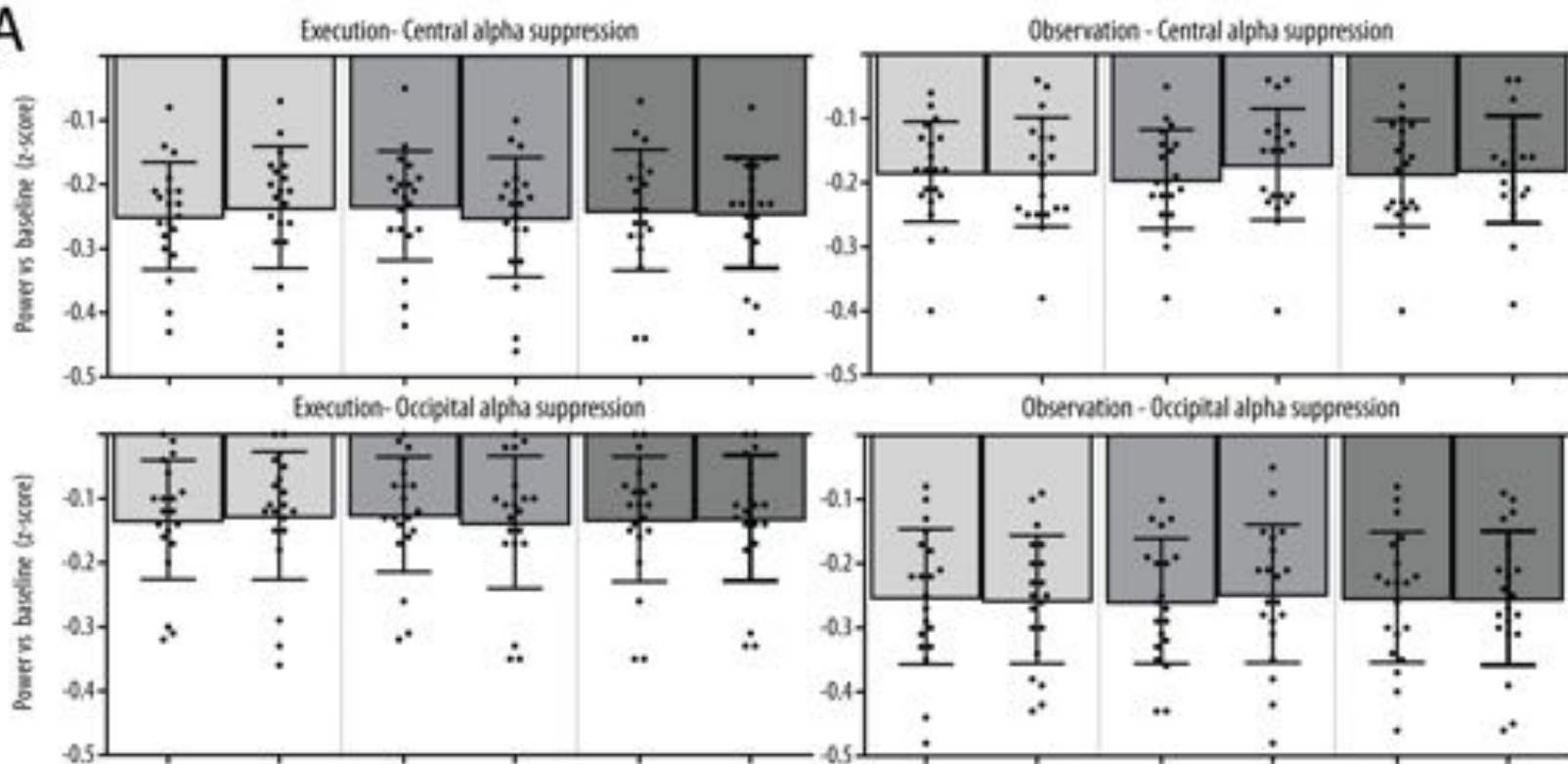
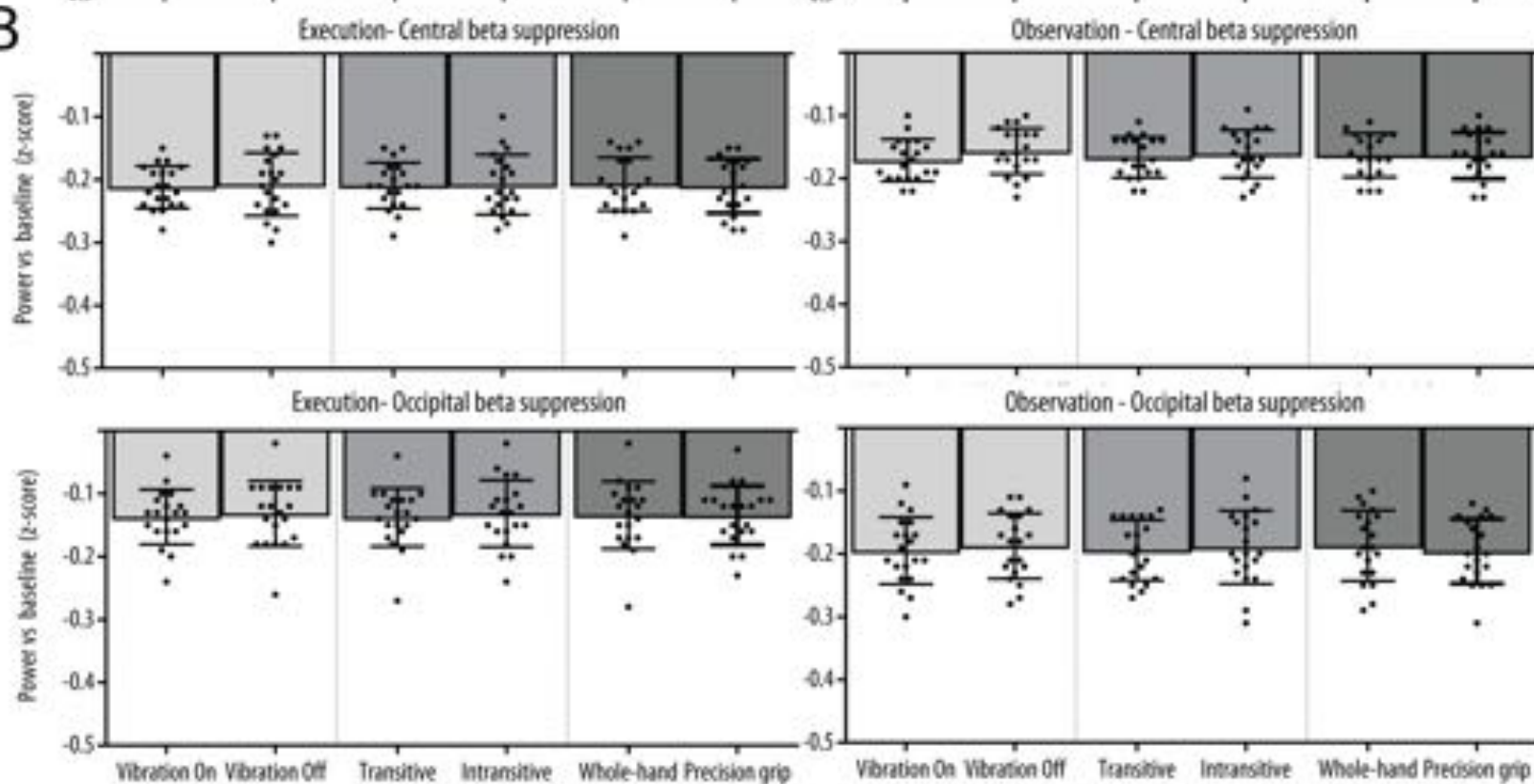


Univariate - Observation - Beta

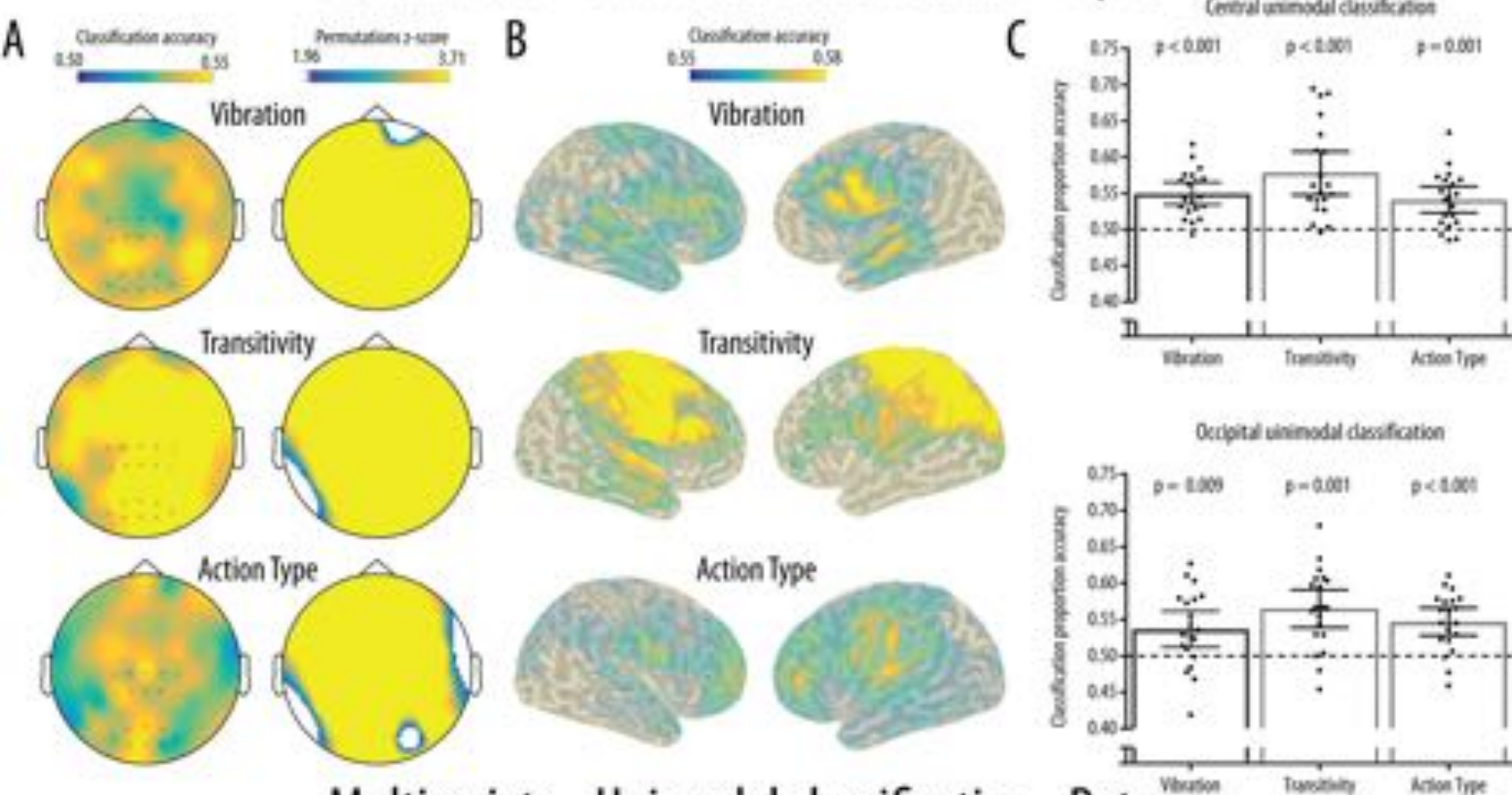


Univariate - Execution - Beta

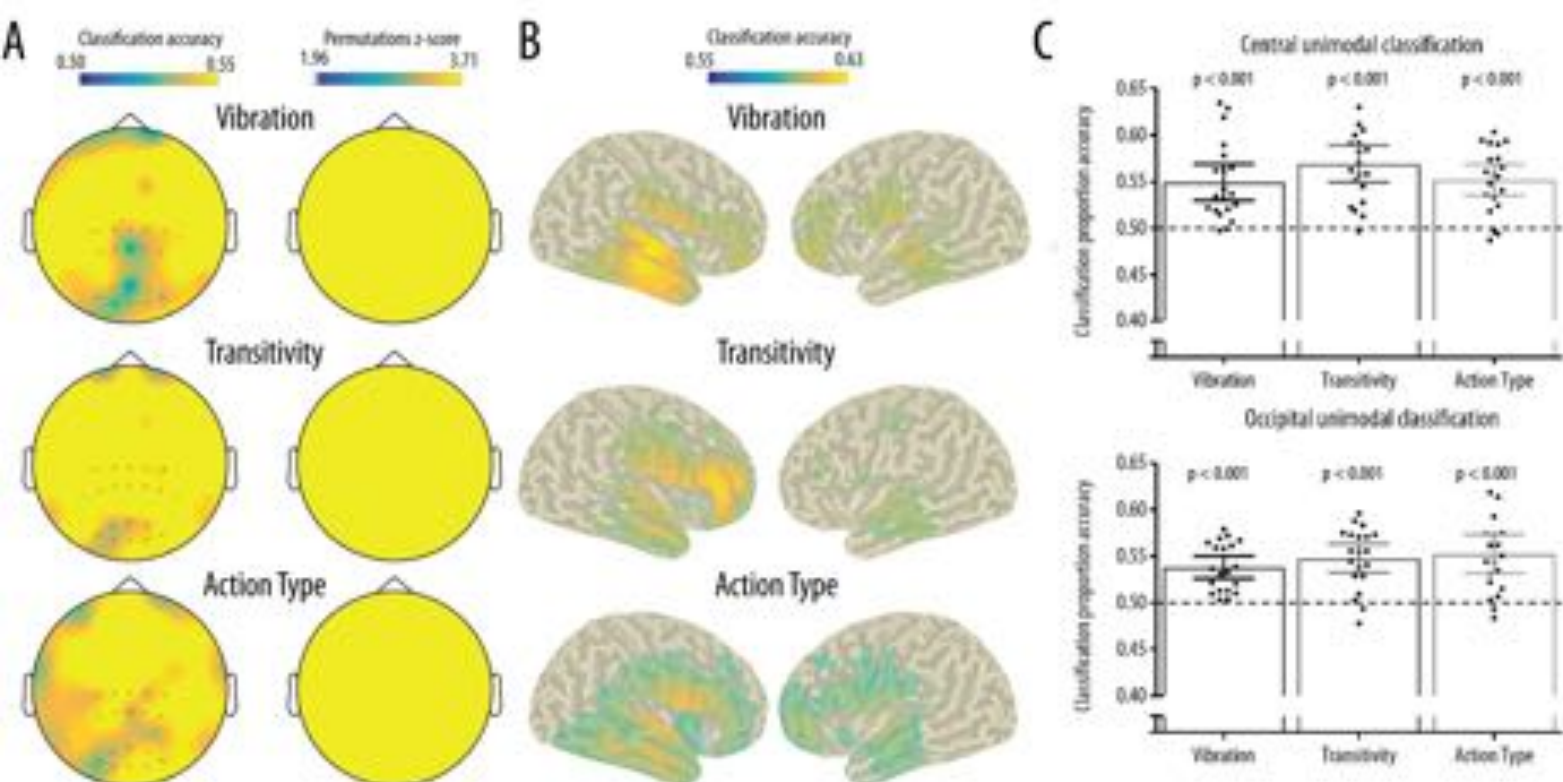


A**B**

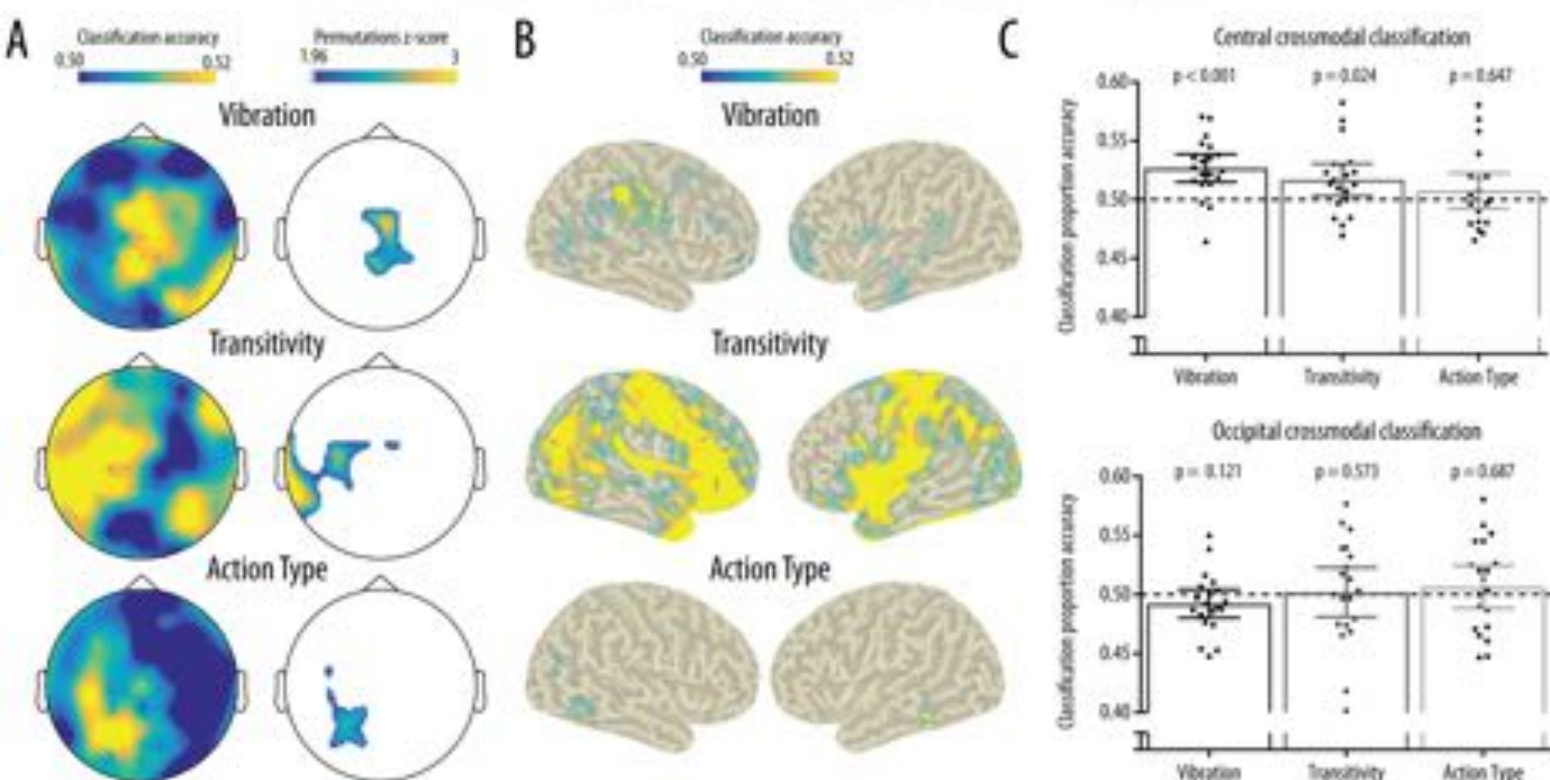
Multivariate - Unimodal classification - Alpha



Multivariate - Unimodal classification - Beta



Multivariate - Crossmodal classification - Alpha



Multivariate - Crossmodal classification - Beta

