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## ***De novo* brain-computer interfacing deforms manifold of populational neural activity patterns in human cerebral cortex**

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- 35

36 **Abstract**

37 Human brains are capable of modulating innate activities to adapt to novel  
38 environments and tasks; for sensorimotor neural system this means acquisition of a rich  
39 repertoire of activity patterns that improve behavioral performance. To directly map the  
40 process of acquiring the neural repertoire during tasks onto performance improvement,  
41 we analyzed net neural populational activity during the learning of its voluntary  
42 modulation by brain-computer interface (BCI) operation in female and male humans.  
43 The recorded whole-head high-density scalp electroencephalograms (EEG) were  
44 subjected to dimensionality reduction algorithm to capture changes in cortical activity  
45 patterns represented by the synchronization of neuronal oscillations during adaptation.  
46 Although the preserved variance of targeted features in the reduced dimensions was  
47 20%, we found systematic interactions between the activity patterns and BCI classifiers  
48 that detected motor attempt; the neural manifold derived in the embedded space was  
49 stretched along with motor-related features of EEG by model-based fixed classifiers, but  
50 not with adaptive classifiers that were constantly recalibrated to user activity. Moreover,  
51 the manifold was deformed to be orthogonal to the boundary by *de novo* classifiers with  
52 a fixed decision boundary based on biologically unnatural features. Collectively, the  
53 flexibility of human cortical signaling patterns (i.e., neural plasticity) is only induced by  
54 operation of a BCI whose classifier required fixed activities, and the adaptation could be  
55 induced even the requirement is not consistent with biologically natural responses.  
56 These principles of neural adaptation at a macroscopic level may underlie the ability of  
57 humans to learn wide-ranging behavioral repertoires and adapt to novel environments.

58 **Significance Statement**

59 We investigated adaption of macroscopic neural activities during brain-computer  
60 interface (BCI) operation to directly map the process of acquiring the neural repertoire  
61 for performance improvement. When the classifier incorporated in BCI was fixed and  
62 based on the desynchronization of neural oscillations, the distribution of activity patterns  
63 (neural manifold) showed the improved separability along with the motor-related  
64 component of electroencephalograms to improve BCI controllability. Meanwhile the  
65 adaptive classifier constantly fitted to current user activity did not elicit such adaptation  
66 of neural activity patterns . Moreover, even the classifiers based on biologically  
67 unnatural model induced the adaptation, captured by deformation of neural manifold.  
68 Neural adaptation processes at a macroscopic level may underlie the ability of humans  
69 to learn wide-ranging behavioral repertoires.

70

71 **Introduction**

72 Human beings can sophisticate motor plans and subsequent actions to dynamically  
73 interact with the external environment (Burdet et al., 2001; Scott, 2004; Todorov &  
74 Jordan, 2002). One surprising demonstration is an adaptation to changes in the  
75 properties of physical interfaces such as the use of novel tools or loss and  
76 augmentation of body parts by tuning distributed sensorimotor circuitries to achieve  
77 smooth interaction with surroundings (Choi et al., 2020; CI Penaloza, 2018; Imamizu et  
78 al., 2000; Kieliba et al., 2021; Mehring et al., 2019; Quallo et al., 2009; Rossi et al.,  
79 2021).

80 The internal representation of sensorimotor adaptation has been sought by  
81 electrophysiology and neuroimaging techniques (Berlot et al., 2020; Diedrichsen et al.,  
82 2005; Karni et al., 1995; Kleim et al., 2004; Nudo et al., 1996). In particular, the primary  
83 motor cortex (M1) exhibits covariance patterns of multiple neural units, namely the  
84 neural manifold which reliably represents ongoing behavior and its correction (Gallego  
85 et al., 2018, 2020; Perich et al., 2018; Shenoy & Kao, 2021). Moreover, direct mapping  
86 of behavior and single neuron activity patterns achieved with brain-computer interfaces  
87 (BCI) revealed monkeys are capable of endogenous modulation of the patterns inside  
88 the manifold, but not those outside (Sadler et al., 2014). Although the conception of the  
89 neural manifold describes cell-neuron level principles of learning within a single local  
90 region (Chaudhuri et al., 2019; Golub et al., 2018; Oby et al., 2019), little is known about  
91 the constraints on the adaptation of the macroscopic sensorimotor system, that is  
92 shaped by the synchronization and desynchronization of net populational neural  
93 activities across multiple brain regions (Fries, 2015; Wander et al., 2013). Because the

94 summation of activity of locally interconnected  $-10^7$  neurons cancels out the property of  
95 a single neuron and only maintains their synchronized activities which mediate  
96 information processing in the human cortical system, the principles governing the  
97 cortical adaptation processes at the macroscopic scale are putatively distinct from the  
98 local unit activities in a single region (Kelso, 2012; Tognoli & Kelso, 2014).

99 To investigate human adaptability at the sensorimotor network level, we used BCI  
100 operation tasks based on scalp electroencephalograms (EEG) with a variety of  
101 incorporated classifiers (Figure 1A). Since users attempted to move a virtual object by  
102 exploring mental actions that effectively modulates EEG signals to control BCI, this  
103 experimental paradigm allows us to examine the relationship between BCI properties  
104 and process in the cortical adaptation (i.e., changes in neural activity patterns to fit the  
105 rule of BCI classifier). As shown in Figure 1B, we specifically hypothesized two distinct  
106 adaptation processes induced to improve BCI operation performance: (i) separation:  
107 rescaling of cortical activity patterns that increases geometric distances between two  
108 brain states and (ii) rotation: deforming of the configuration of two brain states induced  
109 by changes in the whole-brain activity patterns. The former represents changes in the  
110 separability along with the targeted EEG feature and the latter represents rotational  
111 changes in the activity patterns towards perpendicular to the BCI classifier, respectively.  
112 The geometric analysis in the dimensionality-reduced space offers the opportunities to  
113 capture the reorganization of whole-brain neural dynamics.

114 To test whether the cortical adaptation process is influenced by BCI configurations,  
115 we employed three types of BCIs whose classifiers were based on different rules:  
116 model-based, *de novo* and adaptive classifiers. The model-based and *de novo*

117 classifiers were based on fixed scalp EEG feature to induce adaptation of neural activity  
118 patterns. The model-based classifier was based on hand-area motor cortical activities  
119 and users were informed a mental strategy to successfully control BCIs, meanwhile, the  
120 *de novo* classifier was based on temporo-parietal activities and users were encouraged  
121 to explore the suitable strategy (Shibata et al., 2011). The adaptive classifier was  
122 designed to adapt to the current brain activity patterns using the whole-head EEG  
123 signals as input, facilitating the classifier-side adaptation by a block-by block calibration.  
124 We hypothesized the fixed type BCIs require reorganization of whole-brain activity  
125 patterns while the adaptive BCIs rather induce the classifier-side adaptation by  
126 intermittent calibration. Difference in the adaptation process would be characterized by  
127 geometric changes in the low-dimensional representation of neural activity patterns; BCI  
128 operation with fixed types of classifiers would lead the progress in the separation and  
129 rotation because of enhanced discriminability of brain states along with the EEG-feature  
130 for classifier input. Meanwhile, the adaptive BCI would not induce those changes since  
131 the classifier-side constant calibration can optimize the classifier to fit the current brain  
132 state without changing user-side activities.  
133

134 **Materials and Methods**

135 **Participants**

136 Twenty-one neurologically healthy adults (9 females, 12 males, mean age:  $22.6 \pm 3.23$ )  
137 naïve to BCI operation participated in this experiment. The appropriate sample size for  
138 this study was determined by an a-priori power analysis ( $\alpha = 0.05$ ,  $1-\beta = 0.8$ , two-sided  
139 Wilcoxon signed-rank tests) focusing on the deforming effect induced by *de novo* BCI.  
140 The statistical package G\*Power 3 (Faul et al., 2007) was used to estimate the sample  
141 size that shows large Cohen's  $d = 0.90$  reported in the previous EEG-based  
142 neurofeedback literatures (Hayashi et al., 2020; Soekadar et al., 2015).

143 All participants had normal or corrected-to-normal vision and were asked to provide  
144 written informed consent before participating in the experiment. This study was  
145 conducted according to the ethics of the Declaration of Helsinki. The experimental  
146 protocol was approved by the ethical committee of the affiliated organization (Approval  
147 Number: 2020-36).

148

149 **Experimental setup**

150 Participants were seated on a comfortable chair in a quiet room. A display was placed  
151 about one meter in front of the chair to provide task instructions and visual feedback  
152 from BCIs. EEG signals during the experiment were acquired with a 128-channel  
153 HydroCel Geodesic Sensor Net (HCGSN, EGI, Eugene, OR, USA.). The layout of  
154 channels followed the international 10-10 electrode positions shown in Figure 2A (Luu &  
155 Ferree, 2005). The reference channel was set to Cz. The impedance of all channels

156 was maintained below 50 k $\Omega$  throughout the experiment. The EEG data were collected  
157 with a sampling rate of 1000 Hz.

158

### 159 **Experimental procedure**

160 Participants underwent 16 BCI operation blocks comprised of 20 trials. All experimental  
161 procedures were conducted within 2 hours to guarantee the reversibility of any potential  
162 effect of induced unnatural neural plasticity and investigate the initial phase of learning  
163 to operate the BCIs (Hayashi et al., 2020; Marins et al., 2019; Mehler et al., 2019). After  
164 every two blocks, participants were given a break of up to 5 min. Participants were  
165 randomly allocated to one of the three classifiers without informing the configuration of  
166 BCI, the existence of multiple types of classifiers and the allocated type of classifier was  
167 used throughout experiment (See also Online processing of EEG signals).

168 A trial began with a 5-s “Rest” period and a 5-s “Imagine” and a 3-s “Break” period  
169 followed (Figure 2B). During the “Rest” period, participants were instructed to relax  
170 without having any specific thoughts and with opened eyes. In the “Imagine” period,  
171 participants were instructed to perform motor imagery tasks based on the allocated  
172 classifiers. Participants with the model-based and adaptive classifiers imagined  
173 extending the right-hand while those with the *de novo* classifier tried moving a tail to  
174 match the attempted movement with the object on display (Figure 2C). Since tail moving  
175 is not intuitive for human beings, at the beginning of the experiment, participants were  
176 encouraged to explore strategies that enables better controllability of the BCI. The  
177 strategy adopted in each block was freely determined by each participant, but they were  
178 instructed to try to use the same strategy throughout one block to acquire sufficient data

179 and report the adopted strategy at the end of each block. Since the visual feedback for  
180 participants of the model-based and adaptive BCIs were configured to increase grasp  
181 aperture when classifier detect the motor attempt (left panel of Figure 2C), they tried to  
182 keep the virtual hand opened during “Imagine” period and closed “Rest” period.  
183 Likewise, those of *de novo* BCIs were configured to move the tail towards left (right  
184 panel of Figure 2C), participants tried to keep the virtual tail left side of the display  
185 during “Imagine” period and right side “Rest” period. Participants were asked not to  
186 exert overt movement during the feedback period and its compliance was visually  
187 inspected by the experimenters.

188 The performance of each trial was quantified by scores provided by BCI and  
189 participants were encouraged to maximize the culminative sum of score within a block.  
190 Scores were determined by the predicted presence/absence of motor attempt by  
191 classifiers. The absence of motor attempt during “Rest” periods and the presence during  
192 “Imagine” periods increased scores (reward), while the opposite prediction decreased  
193 (punishment). The changing rates of these scores were pertinent to the metrics used for  
194 feedback by each classifier and were regulated linearly to fit the score range from -100  
195 to 100. For the adaptive classifier, the CSP-SVM model was trained with data from the  
196 previous block and the trained model was used in the next block. Note that the first  
197 block of users allocated to the adaptive classifier was identical to that of the model-  
198 based, to collect a dataset for the adaptive classifier training.

199

## 200 **Online processing of EEG signals**

201 To test the initial adaptation process during BCI use, we prepared three types of binary  
202 EEG classifier that detects presence of human motor attempt from based on different  
203 EEG features. The following processing was conducted using MATLAB R2019a (The  
204 Mathworks, Inc, Massachusetts, USA) and Unity (Ver. 2019.2.4f1, Unity Technologies,  
205 USA). Online acquired EEG signals were processed with a 1651-point, minimum-phase,  
206 FIR 8-30 Hz bandpass temporal filter and then processed with one of the three types of  
207 BCI classifiers. Online processed EEG signals were used to detect the presence of  
208 motor attempt with one of the three types of classifiers: model-based, adaptive, or *de*  
209 *novo*. Each classifier was designed with different rules, and electrodes of interest were  
210 defined as shown in Figure 2A. During experiment, users were instructed to use one of  
211 three BCIs at the time course defined as Figure 2B (See also Experimental procedure).

212 The model-based classifier was constructed based on those used in sensorimotor  
213 rhythm (SMR) BCIs (Buch et al., 2008; Kraus et al., 2016). Because accumulated  
214 evidence suggests that event-related desynchronization of SMR (SMR-ERD)  
215 contralateral to the hand that attempted to move reflects the excitability of SM1  
216 (Hummel et al., 2002; Naros et al., 2019; Takemi et al., 2013), EEG signals around the  
217 left SM1 (i.e., channel C3) were only used to detect the attempted movement. In online  
218 processing, a large Laplacian filter was applied to EEG signals from channel C3 to  
219 extract sensorimotor activity (McFarland et al., 1997; Tsuchimoto et al., 2021).  
220 Subsequently, the band power of SMR (SMR-power; 8-13 Hz) was extracted by Fourier  
221 transform with a 1-s window and Hamming window function. The magnitude of SMR-  
222 ERD [dB] was computed from the obtained SMR-power with the following formula:

223

$$\text{ERD}(t) = -10 \log_{10}(P(t) / P_{Ref})$$

224 where  $P(t)$  denotes the signal power of EEG signal at the channel and frequency of  
225 interest, here the SMR-power, at time point  $t$ , and  $P_{Ref}$  denotes the reference power  
226 (Pfurtscheller & Lopes Da Silva, 1999). The reference power  $P_{Ref}$  was calculated from  
227 the middle 3-s period of “Rest” time from the previous trial. Note that the ERD values  
228 were determined independent from classifier parameters. During BCI operation based  
229 on the model-based classifier, movements of the illustrated hand in the display and  
230 performance scores were defined to be linearly related to the SMR-ERD value in the  
231 range of 0 to 10 dB (Figure 2C, Left panel). The range grasp aperture was discretized to  
232 100 steps (0 dB:fully closed, 10dB: fully opened) and scores were calculated by the  
233 integral of SMR-ERD. One may point out the necessity of user-specific model  
234 calibration to identify responsive frequency or channels of interest. However, we used  
235 the identical classifier across participants to avoid the potential confound that the  
236 effectiveness of calibration interacts with learning efficacy.

237 The *de novo* classifier had a fixed classifier plane as did the model-based classifier,  
238 however, its characteristics were biologically unnatural; the *de novo* classifier was  
239 based on EEG signals around the temporo-parietal region (i.e., channel Cz) that are  
240 associated with not only sensorimotor, but also attentional features (Benedek et al.,  
241 2014; Misselhorn et al., 2019). Actively exploring suitable mental strategies, users  
242 attempted to move their body or a visual object on the display during the BCI task.  
243 However, the motor imagery of corresponding body parts at the region (i.e., foot) and  
244 increased attention do not contribute to the spectral power attenuation in the alpha-band

245 (8-13 Hz) required by the classifier. Specifically, since the alpha-band power was  
246 increased by the motor attempt of moving the feet or by internal attention at the targeted  
247 channel (Benedek et al., 2014; Pfurtscheller et al., 2006), such intrinsic responses did  
248 not contribute to the BCI operation, Online computed ERD magnitude with the  
249 procedure identical to that from channel C3 in the model-based classifier was exploited  
250 to decode the absence/presence of attempted movement and index for neurofeedback.  
251 The angle of tail was discretized to 100 steps (0 dB: right limit, 10 dB: left limit). Note  
252 that the rules for object movement were identical to those of the model-based classifier.

253 Lastly, the adaptive classifier was constructed using whole-head scalp EEG signals  
254 based on a common spatial pattern (CSP) algorithm and a support vector machine  
255 (SVM) (Blankertz et al., 2007; Pfurtscheller et al., 2006). To adapt to the current activity  
256 patterns of users, CSP components that maximize the separability of the two conditions  
257 “Rest” and “Imagine” were trained at the end of each block. SVM classifiers were  
258 constructed to perform a binary classification of the two conditions based on 6 CSP  
259 components. Although the CSP-based feature extraction did not employ time-frequency  
260 transformation for spectral power calculation used in the model-based and *de novo*,  
261 users of adaptive BCIs were also required to perform kinesthetic motor imagery which  
262 modulates spectral power of scalp EEG. The posterior probability for a data point  
263 classified as presence of motor attempt was used as an index for neurofeedback; the  
264 index for the adaptive classifier was defined to be linearly related to the posterior  
265 probability in the range of 50% to 100%. Note that the rules for object movement and for  
266 obtaining scores were identical to those in the other two types of classifiers.

267

268 **Evaluation of BCI performance**

269 For each participant, online-calculated scores were individually subjected to linear  
270 regression analysis to summarize whether performance of participant improved over  
271 blocks for each classifier (Gruzelier, 2014; Kober et al., 2018; Witte et al., 2018). The  
272 score obtained during a given block was used as a dependent variable and block  
273 number was used as a predictor valuable. If scores increased during the experiment,  
274 the regression coefficient for the predictor valuable was positive. After the regression  
275 coefficients were derived from scores of each participant, they were subjected to a  
276 group-by-group Wilcoxon rank-sum test with a false discovery rate correction to test  
277 whether the obtained regression coefficients were significantly different from zero  
278 (Benjamini-Hochberg method;(Benjamini & Hochberg, 1995)). If significant positive shift  
279 of the slopes were observed, the result indicated systematic progress of controllability  
280 improvement for the BCI. However, note that the comparison of the learning rate across  
281 groups are not applicable because of the difference in score calculation procedure.  
282 Moreover, to capture the difference in performance at the beginning and end of  
283 experiment, acquired scores were compared with Wilcoxon signed-rank test for first and  
284 last four blocks of each BCI operation (early and late period, respectively).

285

286 **Offline EEG preprocess**

287 The recorded EEG signals were first preprocessed with EEGLAB (Delorme & Makeig,  
288 2004) to reject artifacts and enhance the computational efficiency with downsampling  
289 (Bigdely-Shamlo et al., 2015) The raw EEG data were filtered with a zero-phase 1-45  
290 Hz FIR bandpass filter, downsampled to 100 Hz and bad channels identified by clean

291 raw data plugin were removed from further analysis. The removed channels were  
292 interpolated spherically to minimize a potential bias when re-referencing the electrodes  
293 to a common average reference. Subsequently, large-amplitude artifacts caused by  
294 blinking or head displacement were removed with artifact subspace reconstruction  
295 algorithm (Kothe & Makeig, 2013). The electrodes were then re-referenced to the  
296 common average reference to extract activity specific to the electrodes (McFarland et  
297 al., 1997).

298 The continuous EEG data were then segmented into trials to evaluate the middle 8-s  
299 periods of the online BCI training trials (i.e., the last 4 s of the “Rest” period and the first  
300 4 s of the “Imagine” period). To obtain the independent EEG components of the  
301 segmented dataset, we used adaptive mixture independent component analysis  
302 (AMICA; (Palmer et al., 2011)). Finally, an automatic artifact rejection was applied using  
303 ICLabel that distinguished genuine EEG components from artifacts induced by eye,  
304 muscle, heart, line noise, and channel noises (Pion-Tonachini et al., 2019).

305 To investigate cortical adaptation processes during brain-computer interfacing, the  
306 band-power features were used as a raw-vector that represents instantaneous overall  
307 brain state. Computed band-power from each EEG channel was subdivided into five  
308 functionally distinct frequency bands (Delta: 1-4 Hz, Theta: 4-8 Hz, Alpha: 8-13 Hz,  
309 Beta: 13-31 Hz, Gamma: 31-45 Hz; Hayashi et al., 2019). The averaged band-power  
310 was log-transformed and normalized to the z-score in a trial-by-trial manner to cancel  
311 base-line drifting. Thereby, the original number of dimensions of the feature vector  $D$   
312 was  $D = 129 \times 5 = 645$ . Note that the feature targeted by the model-based and *de novo*  
313 classifiers were included in  $D$ .

314

315 **Feature extraction of EEG-dataset using t-SNE algorithm**

316 The preprocessed EEG dataset (645×11520 matrix) was subjected to a subject-by-  
317 subject t-SNE analysis, which converted the pairwise distances between data points in  
318 the original feature space to conditional probabilities (Van Der Maaten & Hinton, 2008).  
319 The t-SNE algorithm minimized the Kullback-Leibler divergence representing the  
320 distance between the conditional probability in the original and embedded space, where  
321 conditional probability that the data points  $x_i$  and  $x_j$  are neighbors was calculated from  
322 the pairwise distances of input data. In this study, the number of dimensions of EEG  
323 features was reduced to three with a Barnes-Hut variation of t-SNE (Van Der Maaten et  
324 al., 2014) to speed up the computation. Perplexity, that is a hyperparameter of the t-  
325 SNE algorithm, was set to 20 determined empirically with a parameter search of past  
326 EEG data for best separation between the “Rest” and “Imagine” periods. The  
327 hyperparameter was fixed across participants throughout the study after the  
328 determination. After applying t-SNE, the dimensionality-reduced datasets were  
329 subjected to visualization and a similarity analysis, but classification labels (i.e., “Rest”  
330 or “Imagine”) were determined from the original dataset (Figure 3A).

331

332 **The t-SNE-based dimensionality reduction and quantitative analysis in embedded**  
333 **space**

334 Feature extraction using dimensionality reduction is popularly conducted for high-  
335 dimensional neural data across modalities (Cunningham & Yu, 2014; Lord et al., 2019).  
336 The t-SNE algorithm we employed for dimensionality reduction is advantageous for

337 geometric evaluation as it preserves original distances in the embedded space.  
338 Because t-SNE unfolds the nonlinear structure of a given dataset, the linear distance in  
339 the embedded space can be interpreted as an approximation of geometric distance in  
340 the original space. It illustrates how different one brain activity pattern is from another,  
341 however, it should be noted however that to properly interpret the results (1) distance  
342 scales in the embedded space were rearranged and were variable across iterations of t-  
343 SNE, (2) distance scales in different clusters might have differed, (3) direct comparisons  
344 of distances between clusters were not acceptable because distances within two  
345 clusters were arbitrary. To deal with the above concerns, two approaches were adopted:  
346 (1) data points were bridged to prevent the formation of multiple clusters, and (2)  
347 statistical distances, namely Hotelling's t-squared statistical values, were used instead  
348 of Euclidean metrics. Because distances between nearby points are well preserved in  
349 embedded space, the distance scale of distant points were kept similar for enough data  
350 points, which acts as a bridge and prevents the formation of sparse multiple clusters.  
351 We also adopted the concept of "short-circuiting" (Lee & Verleysen, 2005) by  
352 constructing the feature vectors with overlapped time-windows so that points were  
353 smoothly connected, and all data acquired from single participants were subjected to t-  
354 SNE algorithm at once. Thus, distances from point to point shared the same scale  
355 across all points (i.e., only one cluster was generated in embedded space as shown in  
356 Figure 3B).

357 Hotelling's t-squared statistic was adopted as the distance metrics between two group  
358 of points (Hotelling, 1992). Assume  $x$  and  $y$  are two groups of points lying in a  $p$ -  
359 dimensional space,  $n_x$  and  $n_y$  are the numbers of points,  $\bar{x}$  and  $\bar{y}$  are the sample

360 means, and  $\hat{\Sigma}_x$  and  $\hat{\Sigma}_y$  are the respective sample covariance matrices. The Hotelling's t-  
 361 squared statistic was calculated as:

362

$$t^2 = \frac{n_x n_y}{n_x + n_y} (\bar{\mathbf{x}} - \bar{\mathbf{y}})' \hat{\Sigma}^{-1} (\bar{\mathbf{x}} - \bar{\mathbf{y}})$$

$$\hat{\Sigma} = \frac{(n_x - 1)\hat{\Sigma}_x + (n_y - 1)\hat{\Sigma}_y}{n_x + n_y - 2}$$

363

364 Hotelling's t-squared statistic is suitable for measurements of statistical distance in the  
 365 t-SNE-embedded space, as they were invariant to the distance scale. The distribution of  
 366  $t^2$  follows an  $F$ -distribution:

367

$$t^2 \sim \frac{p(n_x + n_y - 2)}{n_x + n_y - p - 1} F_{p, n_x + n_y - 1 - p}$$

368

369 To normalize the distribution, the square root of  $t^2$  was defined as  $tNorm$  and was  
 370 used as the distance measurement in subsequent analyses:

371

$$tNorm = \sqrt{t^2}$$

372

373 The vector representing the directional relationship between two classes was defined  
 374 as a 3D vector  $tVec$ :

375

$$tVec = tNorm \cdot \frac{\bar{\mathbf{x}} - \bar{\mathbf{y}}}{\|\bar{\mathbf{x}} - \bar{\mathbf{y}}\|}$$

376

377 Data points were divided into two classes: “Rest” and “Imagine” according to their  
378 relative times in the trials.  $tNorm$  and  $tVec$  were calculated for these two conditions.

379

### 380 Classifier plane and geometric assessment of EEG data

381 To investigate the influence of BCI classifiers on the cortical adaptation in the t-SNE-  
382 embedded space, the classifier plane and classifier normal vector were linearly  
383 projected into the embedded space (See Figure 3C). A 3D classifier normal vector  
384  $V = [v_1, v_2, v_3]^T$  was calculated as follows, where T denotes a matrix transpose.

$$X = \begin{pmatrix} 1 \\ \vdots \\ Y \\ 1 \end{pmatrix}, \quad \begin{pmatrix} b \\ \vec{v} \end{pmatrix} = (X^T X)^{-1} X^T P$$

$$V = \vec{v} / \|\vec{v}\|$$

385 Then, the equation of the classifier plane is given as follows.

$$v_1 x + v_2 y + v_3 z + b = 0$$

386 assuming  $Y \in \mathbb{R}^{N \times 3}$  are the points in the 3D embedded space (Three dimensions were  
387 represented as  $x, y, z$ , respectively),  $P \in \mathbb{R}^{N \times 1}$  are the original features referred to by the  
388 classifier (model-based: alpha-ERD at C3, *de novo*: alpha-ERD at Cz, adaptive:  
389 classifier score), where  $N$  is the number of points (11520),  $b$  is the intercept  
390 corresponding to the decision boundary of the classifiers. The classifier normal vector  
391 was derived using the ordinary least squares by minimizing the error between the value  
392 of the feature and those estimated from the coordination in the low-dimensional space.  
393 As is shown in Figure 3C,  $tVec$  were projected to the classifier normal vector to evaluate  
394 its geometric relationship against the classifier. The lengths of projection on the

395 classifier vector ( $t\text{Norm}_p$ ) and the angles between  $t\text{Vec}$  and the classifier vector ( $\theta_p$ )  
396 were calculated across classifiers as follows:

397

$$t\text{Norm}_p = t\text{Vec} \cdot V$$

$$\theta_p = \arccos \frac{t\text{Vec} \cdot V}{\|t\text{Vec}\|}$$

398 Because  $t\text{Norm}_p$  reflects the size of component in  $t\text{Vec}$  aligned with the classifier  
399 normal vector, the increase in the  $t\text{Norm}_p$  indicate how two brain states are separated  
400 by the classifier. Meanwhile,  $\theta_p$  indicate how the relative position of the two states is  
401 aligned with the classifier normal vector.

402

#### 403 **Geometry-based analysis in the embedded space**

404 The geometry-based analysis was conducted in the embedded space, as geometric  
405 relationships of the points reflected the similarities in the original space. The transition  
406 process from one brain condition to another (i.e., absence to presence of attempted  
407 movement) was assessed by the spatial arrangement and separability of points from the  
408 “Rest” and “Imagine” periods in the t-SNE dimension (Figure 1). Emergence of the two  
409 temporal phenomena were defined as follows:

410

- 411 • Separation: The separability of the two conditions (Rest and Imagine) increases  
412 with respect to a fixed axis. Separation is interpreted as the enhancement of  
413 specific cortical activity patterns.

414 • Rotation: The relationship of positions in the two conditions changes direction.  
415 Deforming is interpreted as an alteration of a cortical activity pattern that is  
416 adopted as the rotational changes towards perpendicular to the classifier plane  
417 indicates the reconfiguration of activity patterns contributing to BCI performance  
418 improvement.

419 To quantify the two distinct adaptation process, the following metrics were defined.  
420 Scaling and deforming between the  $i$  th and  $j$  th blocks were respectively quantified by  
421 the difference of  $tNorm_p$  and  $\theta_p$ .

422 If adaptation progresses toward the targeted neural activity patterns required to  
423 control BCIs, the  $tNorm_p$  values should be larger while those of  $\theta_p$  should be smaller.  
424 Thus, the calculated values were subjected to the Wilcoxon signed-rank test to compare  
425 the differences between the early and late periods. For adaptive classifiers, as the  
426 classifier plane was obtained from the 2nd block, we defined early period as 2-5 blocks  
427 for the classifier and the classifier normal vector was approximated by the mean of  
428 vectors derived from trained with the previous blocks. We then corrected the alpha-level  
429 with a Bonferroni correction.

430

#### 431 **Cortical source estimation**

432 To localize the source of neural signaling during BCI operation, EEG signals were  
433 subjected to sLORETA analysis for cortical source estimation (Pascual-Marqui, 2002).  
434 Because the motivation for conducting the source analysis was to test whether the  
435 targeted region of the classifier was successfully activated during the late period of BCI

436 training, averaged data from early and late periods were subjected to a non-parametric  
437 permutation test (Nichols & Holmes, 2002).

438

## 439 **Results**

### 440 **Participants learnt BCI operation based on the mental actions**

441 Twenty-one participants operated BCIs with one of three randomly allocated classifiers  
442 that provided scores contingent on BCI. Since culminated sum of scores in a block  
443 represents the overall performance of BCI operation, we tested whether the  
444 performance improvement was systematically observed in participants of each BCI  
445 (Figure 4A). While BCI performance scores from the model-based and adaptive  
446 classifier generally increased over blocks, those for the *de novo* classifier did not.  
447 Regression coefficients of linear regression analysis were computed based on acquired  
448 scores from each participant, using the block numbers as the explanatory variable and  
449 the acquired scores as response variables. Statistical tests to test for computed  
450 regression coefficients revealed significant differences from zero for BCIs based on the  
451 model-based and adaptive classifiers (model-based:  $p = 0.0078$ ,  $d = 1.86$ , adaptive:  $p =$   
452  $0.023$ ,  $d = 0.97$ , *de novo*:  $p = 0.055$ ,  $d = 0.74$ , Wilcoxon rank-sum test, FDR corrected).  
453 The comparison of acquired scores at early and late period indicate significant  
454 difference across groups (Wilcoxon signed-rank test, all  $p < 0.05$ , Figure 4B), indicating  
455 even *de novo* BCI elicits adaptation of participants through training. Note that direct  
456 comparison of the coefficients among classifiers is not possible because scores from  
457 each classifier were computed based on different EEG-features (Figure 4C, Figure 5).  
458 As shown in Figure 4C, the time-frequency representations of scalp EEG signals

459 derived from channels of interest for the fixed classifiers (i.e., C3 channel for model-  
460 based and Cz for *de novo*), qualitatively exhibited the changes in the SMR-ERD  
461 magnitude during motor imagery (from 0 to 4 s) from early to late period of BCI  
462 operation training. For the fixed classifiers using a pre-defined feature for the motor  
463 attempt detection, the spatial representation was visualized by the cortical source  
464 estimation (Figure 5). The corresponding features exhibited sensorimotor activity  
465 corresponding to the feature on interest (i.e., model-based classifier: activity around  
466 contralateral SM1, *de novo* classifier: activity around temporo-parietal region).

467

468 **Geometric quantification of cortical adaptation process revealed distinct**  
469 **adaptation processes to classifier's separating plane**

470 BCI training requires users to control the voluntary control of targeted activity which  
471 classifiers use for motor attempt detection. However, not only the targeted features,  
472 those derived from regions interconnected with the target would also reorganize through  
473 learning (Wander et al., 2013; Corsi et al., 2020). To examine differences in cortical  
474 adaptation processes, we investigated changes in whole-head EEG signals for the early  
475 and late period (first and last 4 blocks of BCI operation, respectively). An example of  
476 data from the model-based classifier BCI is shown in Figure 3A. As the participant  
477 performed the BCI operation, data during attempted movement (blue points) moved  
478 across the classifier plane, where the sign of relative SMR power flips (Figure 3B). In  
479 this case, the defined metrics  $tNorm_p$  and  $\theta_p$  (Figure 3C) respectively increased and  
480 decreased. The classifier normal vector used to calculate those metrics exhibited  
481 statistical significance across blocks and indicated comparable  $R^2$  values across BCI

482 types (Model-based:  $R^2 = 0.23 \pm 0.1$ , *De novo*:  $R^2 = 0.26 \pm 0.2$ , Adaptive:  $R^2 = 0.21 \pm$   
483 0.2).

484 The Figure 6 indicates changes in the norm of  $tVec$  ( $|tVec|$ ) between early and late  
485 period. Because  $|tVec|$  is determined by the distance between the averaged points of  
486 two brain states, its change reflects the overall activity changes including the modulation  
487 of EEG component irrelevant to BCI control. For participants trained with model-based  
488 classifier  $|tVec|$  significantly decreased ( $p = 0.016$ ,  $d = 1.02$ , two-tailed Wilcoxon signed-  
489 rank test) while no systematic changes were observed for other two types (*de novo*:  $p =$   
490  $0.22$ , adaptive:  $p = 0.81$ ), suggesting the whole-brain activation patterns did not exhibit  
491 increased separability in any of three BCIs. However, despite the decrease in the overall  
492 norm of  $tVec$ ,  $tNorm_p$  values, the component of  $tVec$  relevant to the EEG component  
493 used for the motor attempt detection by the classifier (i.e., ERD in alpha-band at  
494 contralateral SM1) significantly increased in the participants of the model-based BCI  
495 (Figure 7A,  $p = 0.016$ ,  $d = 0.71$ ). At the same time,  $\theta_p$  values decreased significantly for  
496 participants trained with both the model-based ( $p = 0.016$ ,  $d = 0.77$ ), indicating the  
497 reorganization of whole-brain activity patterns towards perpendicular to the classifier  
498 plane. Note that the negative values of  $tNorm_p$  observed in some participants of  
499 model-based and *de novo* BCIs are due to the use of fixed classifier normal vectors  
500 derived from whole-experiment data including unsuccessful BCI control.

501 The identical evaluation was conducted for the *de novo* classifiers. Figure 7B depicts  
502 changes in  $tNorm_p$  and  $\theta_p$  against the *de novo* classifier. While no significant  
503 differences were confirmed for  $tNorm_p$  values over blocks ( $p = 0.078$ ),  $\theta_p$  values  
504 significantly decreased ( $p = 0.016$ ,  $d = 1.3$ ), suggesting the partial adaptation to the

505 classifier plane requiring biologically unnatural EEG responses through exploration (i.e.,  
506 ERD in alpha-band at temporo-parietal region).

507 As the classifier planes changed from one block to the next for the adaptive classifiers  
508 trained with the data from the previous blocks, each metric was calculated against the  
509 classifier plane determined with the dataset from the previous block. No significant  
510 differences in  $tNorm_p$  or  $\theta_p$  were confirmed for comparison between the early and late  
511 period for the adaptive classifiers (Figure 7C,  $p = 0.47$ ,  $p = 0.82$ , respectively). Since the  
512 analysis on pre-determined sample size detects statistically significant changes if five  
513 out of seven participants exhibit systematic changes, the result suggests no evidence  
514 in the adaptation of neural activity patterns was found for the adaptive classifier  
515 recalibrated at the end of each block.

516 In summary, short-term BCI operation training elicited different cortical adaptation  
517 processes depending on the BCI types; the model-based and adaptive classifier elicited  
518 group-level systematic learning while *de novo* did not. Meanwhile the two fixed  
519 classifiers induced adaptation of neural activity patterns to improve BCI operation  
520 performance by reorganizing the whole-brain cortical activity patterns evaluated in the t-  
521 SNE space. Further, the performance improvement elicited by the adaptive classifier  
522 was mainly driven by the classifier-side adaptation rather than the cortical adaptation as  
523 suggested by the no evidence of changes in any of metrics of neural activity patterns.

524

## 525 **Discussion**

526 In the present study, participants performed BCI operations with one of three classifiers:  
527 model-based, adaptive, or *de novo*. Because BCI paradigm allows experimenters to set

528 an arbitrary relationship between the BCI model and users (Sadtler et al., 2014),  
529 changes in acquired scores are fully attributed to changes in the targeted feature.  
530 Although learning curve of acquired scores indicated model-based and adaptive  
531 classifiers exhibited significant improvement for BCI control, the adaptation processes  
532 were likely distinct. Each classifier elicited a different cortical adaptation process  
533 consistent with their characteristics; for the model-based classifier the t-SNE analyses in  
534 embedded space revealed decrease in  $|tVec|$  and increases in  $tNorm_p$  that is the  
535 metric for separation of the neural manifold with respect to the axes orthogonal to the  
536 fixed decision boundary. Meanwhile, for the adaptive classifiers, changes in populational  
537 activities were not induced. Lastly, decrease in  $\theta_p$ , that is the metric for deforming effect  
538 reflecting reconfiguration of neural manifold orthogonal to its classifier plane, was  
539 induced by the *de novo* classifier based on biologically unnatural features. Because the  
540 present study focused on the difference in the performance improvement of BCI control  
541 at the initial stage, binary classifiers employed in the three types of BCIs were putatively  
542 suitable for the naïve BCI users to learn its control within short-term period. The findings  
543 would also contribute to the adaptation process to the BCI with multivariate classifiers  
544 whose performance is improved through gradual increase in degree-of-freedom  
545 (Benabid et al., 2019; Edelman et al., 2019).

546 Users of model-based BCI demonstrated overall improvement of acquired scores and  
547 the increase in  $tNorm_p$ . Because  $tNorm_p$  indicates increase in the separability of the  
548 two states to improve performance of BCI operation, its increase suggests scaling effect  
549 along the axis orthogonal to the decision boundary. The systematic increase in  
550 separability was only observed for the model-based classifiers that required the

551 attenuation of SMR derived from contralateral hemisphere to imagined hand while the  
552 model-based BCI induced decrease in the absolute length of  $tVec$ . The contradictory  
553 changes, that decrease in overall norm and increase in norm of the projection to  
554 decoder normal vector, would be explained by the suppression of signaling changes not  
555 beneficial for BCI operation since the model-based BCI determines the presence of  
556 motor attempt only based on the electrode from targeted region (i.e., contralateral SM1).  
557 Such selective modulation of specific component is consistent with motor skill  
558 acquisition (Bassett et al., 2015) as well as previous reports of adaptation of neural  
559 activity patterns during BCI operation (Corsi et al., 2020; Hennig et al., 2021).  
560 Collectively, the scaling effect evaluated by  $tNorm_p$  would be mainly driven by the  
561 selection of activity patterns rather than the emergence of new patterns which elongates  
562 the manifold. The finding about reorganization process of whole-brain activation  
563 patterns, that is concurrent improvement of modulating task-relevant and suppressing  
564 task-irrelevant activities in the early phase of BCI training, is consistent with those  
565 observed for motor learning (Dal'Bello and Izawa, 2021), suggesting utility of the  
566 geometric assessment to evaluate adaptation process. Because the t-SNE analysis  
567 employed in the present study focused on the adaptation along with the axis  
568 perpendicular to the classifier plane, the process of the automation of cortical  
569 activities was not fully investigated in the present study. The more specialized  
570 investigation based on the present finding would be warranted using a large cohort of  
571 populations experiencing BCI operation with the combination of customization of BCI  
572 classifier to fit user-specific SM1 activities (e.g., frequency and channel selection based  
573 on calibration data).

574 Another fixed classifier, namely *de novo* classifier did not elicit the systematic  
575 changes in the  $tNorm_p$ . Although the EEG feature the *de novo* classifier used was  
576 derived from the temporo-parietal alpha activity, participants did not exhibit systematic  
577 adaptation observed in those of the model-based classifier. This difference might have  
578 stemmed from not only the classifier configuration, but also instruction about the task.  
579 Since exploration behavior was encouraged during *de novo* classifier operation, the  
580 instruction may lead association of the specific patterns with better control of BCI and  
581 acquisition of covert mental strategies in an implicit manner through neurofeedback  
582 (Shibata et al., 2011). As motor tasks adapted through such an exploratory strategy  
583 might require more extensive training than recalibrating the existing control  
584 configuration (Choi et al., 2020; Radhakrishnan et al., 2008; Telgen et al., 2014), multi-  
585 day training of the *de novo* BCI operation would induce the sophistication of BCI  
586 operation by adopting exploration strategy (Fujisawa et al., 2019).

587 Rotational effect was quantified by another metric for geometric evaluation,  $\theta_p$  that  
588 indicates the angle between classifier normal vector and  $tVec$ . While the increase in  
589  $tNorm_p$  indicated two brain states became more separable with respect to the features  
590 used in classifiers, the decrease in the  $\theta_p$  indicated the changes in cortical activity  
591 patterns during the BCI operation. Significant changes in  $\theta_p$  were observed for not only  
592 for model-based classifiers but also *de novo*. Although the absence of increase in  
593  $tNorm_p$  was concomitant with that of obtained scores dependent on the targeted EEG-  
594 feature, the cortical adaptation that partly contributed to the *de novo* BCI operation was  
595 probed by  $\theta_p$  changes. As the  $\theta_p$  is the nonlinearly related to  $tVec$  (the overall distance  
596 between the two brain states), the metric is more sensitive to changes in the geometric

597 configuration than  $tNorm_p$  which is linear function of  $tVec$  (See Classifier plane and  
598 geometric assessment of EEG data).

599 One potential limitation of the t-SNE analysis employed in the present study is that  
600 the variance of features explained by the classifier vector becomes relatively low due to  
601 the nature of dimensionality reduction algorithms. Since the high-dimensional brain  
602 activity patterns (645 dimensions) were compressed into 3D spaces, the explained  
603 variance of features by classifier normal vectors became overall 20%. Nevertheless,  
604 because we observed consistent statistical significance of linear regression models  
605 across participants and the preserved variance was sufficient to detect the  
606 reorganization process along with the features targeted by BCIs in keeping with the  
607 univariate analyses on acquired scores during BCI operation, the estimated classifier  
608 normal vectors were statistically reliable representation of features targeted by BCIs.  
609 Given that t-SNE algorithm preserves relative distances of each data point in the  
610 original space, we believe the t-SNE analysis would be beneficial as a complementary  
611 analysis for univariate analyses to evaluate the adaptation process at the whole-brain  
612 level.

613 The present study demonstrated neuroplastic changes in the whole-brain  
614 macroscopic activity patterns induced by brain-computer interfacing in the first 2 hours.  
615 Although the primary focus of the present study was to detect the differential interaction  
616 of human brain and classifiers at the early period, the difference elicited by long-term  
617 use is not mentioned in the study. While previous BCI studies have demonstrated the  
618 long-term co-adaptation is one successful strategy for efficient training (Perdikis et al.,  
619 2018; Silversmith et al., 2020), however, the limited amount of training period in the

620 study did not elicit the adaptation of neural activity patterns by the adaptive classifier  
621 use. Such differences in the adaptation process depending on time scale are warranted  
622 in the further investigation.

623 Although the flexibility of the human brain enabled adaptation to model-based  
624 classifiers and partly to the *de novo*, the adaptive classifier did not elicit adaptation of  
625 neural activity patterns, manifested by the absence of any changes in geometric  
626 assessment at least the early stage of BCI operation training. It would be because the  
627 adaptive BCI enhanced its performance by classifier-side adaptation, that maximized  
628 the separability of two brain states for the current data by classifier reconfiguration. In  
629 contrast to the previous studies demonstrating co-adaptation of brain and classifiers  
630 using the trial-by-trial classifier adaptation (Wolpaw and McFarland, 2004; Orsborn et  
631 al., 2014), the block-by-block calibration procedure waived the previously optimized  
632 parameters and reconstructed an entirely new model, the classifier-side adaptation  
633 could have been dominant. As the user did not receive neurofeedback based on the  
634 constant rule (i.e., parameters of the classifier) putatively due to the abrupt changes in  
635 the classifier parameters as well as the CSP features, it could have achieved the high  
636 separability of two brain states without engaging cortical adaptation process yet  
637 interfered the user's attempt to adapt to the classifier. In summary, fixation of the  
638 classifier plane is an essential element for inducing neural plasticity via a brain-  
639 computer interaction based on macroscopic neural populational activities, and  
640 adaptation to a BCI based on unnaturalistic features without the instruction of suitable  
641 strategies for control is partly possible in the initial stage of BCI operation training. This

642 demonstration may in part explain human adaptability to external environment that  
643 continuously changes over time, underlying the flexibility of our motor performance.

644

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891 **Figure 1 Conceptual illustration of neural adaptation process induced by brain-**  
892 **computer interfacing**

893 A: Setup of a brain-computer interface. Online acquired scalp electroencephalograms  
894 were fed into a classifier to detect the presence/absence of attempted movement.  
895 Predicted brain state was shown to participants as movement of visual object on  
896 display.

897 B: Conceptual visualization of cortical adaptation. Scaling adaptation reflects  
898 improvement in voluntary regulation of a specific component. If the centers of gravity  
899 determined from datapoints in two conditions are separated after brain-computer  
900 interfacing, it suggests the separability of two conditions is enhanced by adaptation.  
901 Deforming adaptation suggests that activity patterns are allocated to a specific brain  
902 state in order to adapt to the classifier. If the geometric relationships between two  
903 conditions are deformed with respect to a specific axis, it suggests the adaptation  
904 process progressed such that the two conditions are separated along the axis.

905

906 **Figure 2 Experiment setup and protocol**

907 A: Electrode locations. The three classifiers used in the study had different channels of  
908 interest. The model-based classifier used only channel C3 indicated in blue around the  
909 left sensorimotor cortex. The adaptive classifier used whole-head EEG channels  
910 (purple) to construct a common spatial pattern. The *de novo* classifier used only the Cz  
911 channel, shown here in green.

912 B: Experimental protocol and time course of a trial

913 C: Visual feedback object. For the model-based or adaptive classifiers, an illustration of  
914 a hand was shown that matched the attempted movements of the users while an

915 illustration of a tail was used in the *de novo* task to encourage users to acquire novel  
916 mental actions that enhanced controllability of the BCI.

917

918 **Figure 3 low dimensional visualization of EEG data by t-SNE**

919 A: Examples of t-SNE-based visualization of datasets from a representative participant  
920 in each classifier. Each axis represents results of the t-SNE analysis, which generates  
921 three axes from input data. Blue points represent data from the Imagine period and red  
922 ones are those from the Rest period.

923 B: Changes in geometric relationships between dataset and classifier plane. As training  
924 progressed, the geometric relationship of points from two brain states changed with  
925 respect to the classifier plane (black plane). The large points indicate the centers of  
926 gravity of points from each brain state. The black line orthogonal to the classifier plane  
927 is the classifier normal vector (see also Figure 3D)

928 C: An example of t-SNE-based data visualization in embedded space (Model-based  
929 classifier user). Each datapoint is colored with its SMR-ERD value derived from the C3  
930 electrode around the left sensorimotor cortex. The black plane represents the classifier  
931 plane (see also equation 2.9 for mathematical details). The large points indicate the  
932 centers of gravity of points from each brain state. The black line orthogonal to the  
933 classifier plane is the classifier normal vector (see also Figure 3D).

934 D: The t-SNE-based quantification of the adaptation process with respect to the  
935 classifier plane.  $tNorm_p$  is defined as a component of  $tVec$  with respect to the classifier  
936 vector, while  $\theta_p$  is defined as a subtended angle between  $tVec$  and the classifier vector.

937

938 **Figure 4 Changes in BCI operation performance and time-frequency**  
939 **representations of scalp electroencephalogram signals**

940 (A) Group results of performance scores from users of model-based, *de novo* and  
941 adaptive classifiers. Solid lines indicate mean values while shaded areas represent 1  
942 standard error across participants. (B) Changes in the acquired scores during BCI  
943 operation. (C) Changes in time-frequency representations of scalp  
944 electroencephalogram signals from representative channels.

945

946 **Figure 5 Spatial activity patterns during brain-computer interfacing**

947 Results of source estimation analysis from representative participants. The colored  
948 regions indicate voxels where activities were significantly different during Rest and  
949 Imagine periods ( $p < 0.05$  unc.). Areas colored with blue and green indicate those for  
950 model-based and *de novo* classifiers, respectively. While significant voxels were  
951 localized around the contralateral hemisphere of the imagined hand for the model-  
952 based classifier, those for the *de novo* classifier were located bilaterally, including in the  
953 pre/post central gyrus and supplementary motor area (peak voxel was in the postcentral  
954 gyrus, [MNI coordinates: -40, -25, 45]). Note that a representative source estimation for  
955 the adaptive classifier is not shown due to variable activity patterns among participants.

956 sLoreta analyses of statistical non-parametric mapping for estimated cortical sources  
957 of band power in the alpha band (8-13 Hz). Areas colored with blue and green indicate  
958 those from model-based and *de novo* classifiers, respectively. Masks superimposed on  
959 a standard brain template were visualized by MRICroGL  
960 (<https://www.mccauslandcenter.sc.edu/mricrogl/home>).

961

962 **Figure 6 Overall changes in distance between brain states**

963 Changes over time in the norm of  $tVec$  for participants operating under the model-based  
964 classifier (A), the *de novo* classifier (B), and the adaptive classifier (C).

965

966 **Figure 7 Quantitative comparison of cortical adaptation processes in embedded**

967 Changes over time in  $tNorm_p$  and  $\theta_p$  for participants operating under the model-based  
968 classifier (A), the *de novo* classifier (B), and the adaptive classifier (C).

969













