

1 **Decoding Internally- and Externally-Driven Movement Plans**

2 Abbreviated title: Internally- and Externally-Driven Movements

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4 Giacomo Ariani<sup>1</sup>, Moritz F. Wurm<sup>1</sup>, & Angelika Lingnau<sup>1,2,3\*</sup>

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6 1: Center for Mind/ Brain Sciences (CIMeC), University of Trento, Via delle Regole 101, 38100 Mattarello  
7 (TN), Italy

8 2: Department of Cognitive Sciences, University of Trento, Corso Bettini, 31, 38068 Rovereto (TN), Italy

9 3: Department of Psychology, Royal Holloway University of London, TW20 0EX Egham, Surrey, UK

10  
11 **\*Corresponding author:**

12 Angelika Lingnau, [angelika.lingnau@unitn.it](mailto:angelika.lingnau@unitn.it); [angelika.lingnau@rhul.ac.uk](mailto:angelika.lingnau@rhul.ac.uk)

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24 analyzed data; and G.A., M.W., and A.L. wrote the manuscript.

25

26 **ABSTRACT**

27 During movement planning, brain activity within parieto-frontal networks encodes information about  
28 upcoming actions that can be driven either externally (e.g. by a sensory cue) or internally (i.e. by a  
29 choice/decision). Here we used multivariate pattern analysis (MVPA) of functional magnetic resonance  
30 imaging (fMRI) data to distinguish between areas that represent (1) abstract movement plans that  
31 generalize across the way in which these were driven, (2) internally-driven movement plans, or (3)  
32 externally-driven movement plans. In a delayed-movement paradigm, human volunteers were asked to  
33 plan and execute three types of non-visually guided right-handed reaching movements towards a central  
34 target object, using a precision grip, a power grip, or touching the object without hand preshaping. On  
35 separate blocks of trials, movements were either instructed via color cues (Instructed condition), or chosen  
36 by the participant (Free-Choice condition). Using region-of-interest (ROI)-based and whole-brain  
37 searchlight-based MVPA, we found abstract representations of planned movements that generalize across  
38 the way these movements are selected (internally- vs externally-driven) in parietal cortex, dorsal premotor  
39 cortex and primary motor cortex contralateral to the acting hand. In addition, we revealed representations  
40 specific for internally-driven movement plans in contralateral ventral premotor cortex, dorsolateral  
41 prefrontal cortex, supramarginal gyrus, and in ipsilateral posterior parieto-temporal regions, suggesting  
42 that these regions are recruited during movement selection. Finally, we observed representations of  
43 externally-driven movement plans in bilateral supplementary motor cortex and a similar trend in pre-  
44 supplementary motor cortex, suggesting a role in stimulus-response mapping.

45 **SIGNIFICANCE STATEMENT**

46 The way the human brain prepares the body for action constitutes an essential part of our ability to interact  
47 with our environment. Previous studies demonstrated that patterns of neuronal activity encode upcoming  
48 movements. Here we used multi-variate pattern analysis of human fMRI data to distinguish between brain  
49 regions containing movement plans for instructed (externally-driven) movements, areas involved in  
50 movement selection (internally-driven), and areas containing abstract movement plans that are invariant to  
51 the way these were generated (i.e. that generalize across externally- and internally-driven movement  
52 plans). Our findings extend our understanding of the neural basis of movement planning, and have the  
53 potential to contribute to the development of brain-controlled neural prosthetic devices.

54 **INTRODUCTION**

55 In daily life we continuously select which movements to plan and execute. Parieto-frontal regions have  
56 been implicated in the planning, execution and online control of eye and hand movements in a number of  
57 human (Connolly et al., 2002; Filimon, 2010; Beurze et al., 2009; Leoné et al., 2014; Gallivan et al., 2011a,  
58 2011b, 2013a; Binkofski et al., 1999; Fabbri et al., 2014; Barany et al., 2014; Cavina-Pratesi et al., 2010;  
59 Tunik et al., 2005; Glover et al., 2012; Brandi et al., 2014; Gallivan & Culham, 2015) and monkey (Afshar et  
60 al., 2011; Andersen & Cui, 2009; Fattori et al., 2010; Hoshi & Tanji, 2006; Lehmann & Scherberger, 2013;  
61 Townsend et al., 2011) studies. Furthermore, pre-movement activity in both parietal and frontal regions  
62 has been shown to encode different hand configurations (Raos et al., 2004, 2006; Murata et al., 2000;  
63 Begliomini et al., 2007; Fluet et al., 2010; Gallivan et al., 2011a; Tunik et al., 2007; Verhagen et al., 2013).

64 Movements can be planned either on the basis of external cues in our environment (externally-  
65 driven), or in the absence of such cues (internally-driven). While it has been reported that the same  
66 parieto-frontal areas involved during externally-driven movements are recruited during internally-driven  
67 movements in monkeys (Pesaran et al., 2008; Cui & Andersen, 2007; Cisek & Kalaska, 2005, 2010), no  
68 previous study directly compared the planning of internally- and externally-driven movements in humans.  
69 Studies that compared externally- and internally-driven movements did not intend to separate movement  
70 planning from execution (Bode et al., 2013; Oliveira et al., 2010; Zhang et al., 2012). By contrast, studies  
71 separating between planning and execution focused on externally-driven movements and thus did not  
72 allow distinguishing between internally- and externally-driven movements (Bernier et al., 2012; Beurze et  
73 al., 2009; Gallivan et al., 2011a, 2011b, 2013a; Pertzov et al., 2011).

74 Here we aimed to distinguish between brain regions representing abstract movement plans that  
75 are neither tied to specific external cues nor to internally-driven decisions, and brain regions representing  
76 movement plans specific for internally-driven or externally-driven movements (Fig. 1A). We asked  
77 participants to perform a delayed-movement paradigm in which they had to plan and execute one of three  
78 different movements (i.e. reach to grasp with a precision grip, with a power grip, or reach to touch) toward  
79 a single centrally-located object (Fig. 1B). On each trial, a visual cue either instructed to plan a specific  
80 movement as instructed by the cue (Instructed condition, i.e. externally-driven), or it indicated to select  
81 and plan one of the three movements (Free-Choice condition, i.e. internally-driven; Fig. 1C). We used  
82 support-vector-machine (SVM)-based MVPA of fMRI data to compare the decoding of upcoming externally-  
83 and internally-driven movements. To examine abstract representations of movement plans that generalize  
84 across the planning conditions, we used cross-condition classification, i.e. training a classifier to distinguish  
85 between upcoming movements on the basis of externally-driven trials, and testing on internally-driven  
86 trials, and vice versa.

87 We reasoned that areas containing abstract movement plans should show movement selectivity  
88 that generalize across the planning condition. By contrast, areas involved in action selection should show

89 movement selectivity in the Free-Choice but not in the Instructed condition. Finally, areas involved in the  
90 processing of sensory cues and/ or the mapping between such cues and the corresponding movements  
91 should show movement selectivity in the Instructed, but not in the Free-Choice condition.

92 << Figure 1 >>

### 93 **MATERIALS AND METHODS**

94 *Participants.* Twenty-five right-handed volunteers (12 males, 13 females; mean age: 27.2 years; age range:  
95 21-54 years) took part in the study. All participants were neurologically intact and had either normal or  
96 corrected-to-normal vision. The experimental procedures were approved by the ethics committee at the  
97 University of Trento. Participants gave written informed consent and were paid for their participation.  
98 Seven participants were subsequently excluded from data analysis: one due to technical problems with  
99 video recordings (see *Setup*), one due to not completing the experimental session, and five due to severe  
100 head motion. Rapid (i.e. taking place within one volume) head motion was detected on the basis of the 3  
101 translation and rotation parameters resulting from 3D motion correction (cut-off criterion: > 1 mm for  
102 translation, > 1 degree for rotation). Overall, 18 participants were included in the successive analyses.

103

104 *Setup.* Visual stimuli (i.e. fixation cross and fixation dot) were back-projected onto a screen (frame rate: 60  
105 Hz; screen resolution: 1024 × 768 pixels; mean luminance: 109 cd/m<sup>2</sup>) via a liquid crystal projector (OC EMP  
106 7900, Epson Nagano, Japan). Participants viewed the screen binocularly through a mirror mounted on the  
107 head coil (Fig. 1D). The screen was visible as a rectangular aperture of 17.8° x 13.4°. The auditory go-signal  
108 was delivered via MR-compatible headphones.

109 Participants performed unimanual (right hand only) reach-to-grasp movements (Fig. 1B) toward a  
110 single, centrally located object (according to each participant's sagittal midline) mounted on top of a  
111 workspace that consisted of a transparent plexiglas board attached to the scanner bed above the waist of  
112 the participant (Fig. 1D). The target object consisted of two custom-made square pieces of wood, glued on  
113 top of each other (Fig. 1D). To exclude uncontrolled visual stimulation by the sight of the own hands and  
114 the object, or systematic eye movements towards the object, participants were scanned in a conventional  
115 fMRI configuration (i.e., horizontally, without tilting the head towards the body; Fig. 1D) and were  
116 instructed to maintain fixation throughout the experiment. This precluded direct viewing of their own  
117 limbs, or the target object, while performing the task without visual feedback.

118 An MR compatible response button (Lumina LP 400, Cambridge Research Systems), attached to a  
119 custom belt around the waist, was pressed by the participant with the knuckles when at rest (home  
120 position, Fig. 1D). A microcontroller board (Arduino Uno) connected to the Lumina Controller positioned  
121 outside the magnet room was used to signal the release of that button. This time stamp was used to  
122 measure movement onset time.

123 To enable movements as comfortable as possible, the position of the workspace and the response  
124 button were adjusted individually to match each participant's arm length (mean distance hand-object: 16.6  
125 cm). Head and trunk movements were minimized by stabilizing the head and the upper right arm with foam  
126 blocks and cushions.

127 To monitor movement execution, we recorded each experimental session using an MR-compatible  
128 digital video camera (VP-D15i; Samsung Electronics) mounted on a tripod in a corner of the MR room  
129 (outside the 0.5-mT line). Stimulus presentation, response collection, and synchronization with the scanner  
130 were controlled using "ASF" (Schwarzbach, 2011), based on the Matlab Psychtoolbox-3 for Windows  
131 (Brainard, 1997).

132

133 *Design.* We used a mixed design with the factors *planning condition* (Instructed, Free-Choice) and  
134 *movement type* (precision grip, PRG; power grip, PWG; touch, TCH; Fig. 1B). *Planning condition* was  
135 blocked, *movement type* was randomized within blocks. In Instructed blocks, each movement type  
136 occurred equally often (3 times), and the color of the fixation cross indicated which movement to perform.  
137 In Free-Choice blocks, participants were instructed to choose one of the three movement types with no  
138 restrictions.

139

140 *Procedure.* To temporally isolate the neural processes associated with movement planning from movement  
141 execution, we used a delayed-movement paradigm (Gallivan et al., 2011a, 2011b, 2013a; Andersen &  
142 Buneo, 2002; Beurze et al., 2009; Fig. 1C). Each trial started with a grey fixation dot lasting for a variable  
143 amount of time that served to alert participants of the upcoming trial. The duration of the fixation dot was  
144 chosen from a geometric distribution ( $p = 0.3$ ; 2000 - 6000 ms, in steps of 500 ms). The fixation dot was  
145 followed by a colored fixation cross for 500 ms, either instructing the type of movement to perform  
146 (Instructed condition), or indicating to select one of the movements (Free-Choice condition). The colored  
147 fixation cross was followed by a jittered inter-stimulus-interval (ISI; Planning phase) independently chosen  
148 from a geometric distribution with the same parameters as described above. At the end of the delay period  
149 an auditory signal (duration: 100 ms, frequency: 350 hz, amplitude: 0.6) provided the GO-cue to start the  
150 movement (Execution phase, 2500 ms), and to return to the home position after completion of the  
151 movement. Participants were asked to keep the hand still and relaxed in the *home* position throughout all  
152 the phases of the trial apart from the Execution phase. Reaction times were defined as the time when the  
153 response button was released time-locked to the GO-cue.

154 While in the Instructed condition different color cues corresponded to different movement types,  
155 the cue always had the same, non-informative, color in the Free-Choice condition. We used two sets of  
156 color-cue assignments that were balanced across participants. Each participant completed a single  
157 experimental session consisting of a practice session outside the scanner (~20 min), the structural scan (~5

158 min), and 10 functional runs (~6 min each). Each functional run started and ended with 15 sec rest and  
159 contained 4 blocks of trials (2 blocks per planning condition) separated by 15 sec rest each. Between the  
160 second and the third block a longer rest period (25 sec) allowed participants to relax their right arm, wrist  
161 and hand. The order of block types (I = Instructed; F = Free-Choice) was pseudo-randomized such that the  
162 first two (or second two) blocks could never be of the same type (i.e., IFIF, FIFI, IFFI, or FIIF). Each block (~60  
163 sec) consisted of 9 trials, for a total of 360 trials per participant. For the Instructed condition, after  
164 excluding error trials, we had an average of 58.70 (range: 50-60) repetitions per movement type and  
165 planning condition per participant. For the Free-Choice condition, the number of trials per movement type  
166 depended on the choices of the participant, with an average of 59.68 (range: 35-81) repetitions per  
167 condition per participant (see *Multivariate pattern classification analysis* section for further details).

168

169 *Data acquisition.* Functional and structural data were collected using a 4T Bruker MedSpec Biospin MR  
170 scanner and an 8-channel birdcage head coil. Functional images were acquired with a T2\*-weighted  
171 gradient-recalled echo-planar imaging (EPI) sequence. Acquisition parameters were a TR (time to repeat) of  
172 2000 ms; voxel resolution, 3 x 3 x 3 mm; TE (time to echo), 33 ms; flip angle (FA), 73°; field of view (FOV),  
173 192 x 192 mm; gap size, 0.45 mm. We used 28 slices, acquired in ascending interleaved order, slightly tilted  
174 to run approximately parallel to the calcarine sulcus. The number of volumes acquired in the main  
175 experiment for each functional run varied according to the length of variable delay periods (range: 178-183  
176 volumes). Before each functional run, we performed an additional scan to measure the point-spread  
177 function (PSF) of the acquired sequence, which served for distortion correction, expected with high-field  
178 imaging (Zaitsev et al., 2004). To be able to coregister the low-resolution functional images to a high-  
179 resolution anatomical scan, we acquired a T1-weighted anatomical scan (magnetization-prepared rapid-  
180 acquisition gradient echo; TR: 2700 ms; voxel resolution: 1 x 1 x 1 mm; TE: 4.18 ms; FA: 7°; FOV: 256 x 224  
181 mm; 176 slices; generalized autocalibrating partially parallel acquisition with an acceleration factor of 2;  
182 inversion time: 1020 ms).

183

#### 184 **Data analysis**

185 *Behavioral analyses.* We measured reaction time (RT) as the time to release the response button (see  
186 *Procedure*) with respect to the auditory GO-cue. Moreover, we analyzed video recordings of the  
187 experimental sessions to ensure that participants performed the movements correctly, and to know which  
188 movements were performed during the Free-Choice condition. Trials were considered errors either when  
189 performed incorrectly (i.e., incorrect hand preshaping; temporal anticipation: RT < 100 ms; reaction time  
190 timeout: RT > 1500 ms) or, in the Instructed condition only, when participants executed a movement that  
191 was different from the one instructed by the cue. Using the videos, we also counted the number of correct  
192 trials per movement type, of particular importance for the Free-Choice condition. Next, to potentially

193 detect participants that showed stereotyped selections (i.e. cognitive strategies) or excessively frequent  
194 movement choices, we created a transition matrix that showed the number of times each movement  
195 followed any other (3-by-3 matrix,  $trial_n \times trial_{n+1}$ ). This allowed us to calculate a measure of  
196 randomness (i.e. entropy) for movement selection in Free-Choice trials (separately per participant and run),  
197 the Shannon's Entropy (Uncertainty) index (Shannon, 1948):

$$H(X) = - \sum_{i=1}^n p(x_i) \log_b p(x_i)$$

198 where  $X$  is a random variable with  $n$  outcomes  $\{x_1, \dots, x_n\}$ , and  $p(x_i)$  is the probability mass function of the  
199 outcome  $x_i$ . Shannon's Entropy index ( $H$ ) ranges from 0 to  $\log_2 n$ , where  $n$  is the number of states or  
200 possible outcomes.

201

## 202 **fMRI data analysis**

203 *Preprocessing.* Data were preprocessed and analyzed using BrainVoyager QX 2.8.0 (BrainInnovation,  
204 Maastricht, The Netherlands) in combination with the BVQX Toolbox and custom software written in  
205 Matlab R2012b (MathWorks, Natick, MA, U.S.A.). To correct for distortions in geometry and intensity in the  
206 echo planar imaging (EPI) images, we applied distortion correction on the basis of the PSF (see *Data*  
207 *acquisition*; Zeng & Constable, 2002). To avoid T1 saturation, we discarded the first 4 volumes. The first  
208 volume of the first functional run of each participant was aligned to the high-resolution anatomy (6 rigid-  
209 body transformation parameters). Next, we performed 3D motion correction (trilinear interpolation for  
210 estimation and sinc interpolation for resampling) using the first volume of the first run of each participant  
211 as reference, followed by slice timing correction (ascending interleaved even-odd order) and high-pass  
212 temporal filtering (3 cycles per run). Spatial smoothing was applied with a Gaussian kernel of 8 mm full-  
213 width half maximum (FWHM) for univariate analysis only. For successive group analysis, both functional  
214 and anatomical data were transformed into a common Talairach space, using trilinear interpolation.

215

216 *Univariate analysis (GLM).* To localize brain areas preferentially involved in movement preparation, we  
217 computed a group random-effects (RFX) general linear model (GLM) analysis in the volume. To avoid  
218 making assumptions about the shape of the HRF during the Planning phase, we used a deconvolution  
219 analysis, estimating the amplitude of the BOLD signal separately for each predictor and time point (TR). We  
220 created six (2 planning conditions x 3 movement types) predictors both for the Planning and Execution  
221 phases, and 1 predictor modelling the baseline between the first and second half of each run, leading to 13  
222 (predictors) x 8 (time points) = 104 predictors. This led to independent estimates of the BOLD amplitude for  
223 each condition and time point resulting from the deconvolution analysis. Parameters from 3D motion  
224 correction (translation and rotation) and regressors for error trials (modelled separately for each time  
225 point) were also included in the model as predictors of no interest. For each voxel, the average of the



226 estimated beta-value at the 3<sup>rd</sup> and 4<sup>th</sup> time points (i.e. 4 to 8 sec after the onset of the planning cue) was  
227 used both for uni- and multivariate analyses (for a similar procedure, see Eisenberg et al., 2010).

228 We aimed to identify regions of interest (ROIs) commonly reported to be involved in the planning  
229 and execution of prehension movements (see Beurze et al., 2009; Gallivan et al., 2011a, 2011b, 2013a;  
230 Fabbri et al., 2014; for a review see Turella & Lingnau, 2014). To do so, we contrasted the Planning phase  
231 against the Baseline [Planning > Baseline] (Fig. 2), collapsing across the two planning conditions. The  
232 resulting volumetric statistical map was corrected for multiple comparisons using a False-Discovery-Rate  
233 (FDR) < 0.05 and projected on the group-averaged surface mesh for visualization (Fig. 2A).

234

235 *ROI definition.* To identify individual ROIs objectively, we followed a similar procedure as recently used by  
236 Oosterhof, Tipper, & Downing (2012a). In brief, we first manually outlined the activations individuated  
237 through the RFX-GLM contrast [Planning > Baseline] on the group-averaged surface mesh (for details on the  
238 creation of the group-averaged surface mesh, see *Brain segmentation, mesh reconstruction, and cortex-*  
239 *based alignment*), roughly circumscribing the ROIs around known anatomical landmarks (see also Gallivan  
240 et al., 2011a, 2011b, 2013a). Specifically, we used the following criteria:

- 241 • *Primary motor cortex (M1)*: around the hand-knob area in the anterior bank of the central sulcus;
- 242 • *Dorsal premotor cortex (PMd)*: at the junction of the superior frontal sulcus and the precentral  
243 sulcus;
- 244 • *Ventral premotor cortex (PMv)*: slightly inferior and posterior to the junction of the inferior frontal  
245 sulcus and the precentral sulcus;
- 246 • *Anterior intraparietal sulcus (aIPS)*: on the anterior segment of the intraparietal sulcus, at the  
247 junction with the postcentral sulcus;
- 248 • *Middle intraparietal sulcus (mIPS)*: on the middle segment of the intraparietal sulcus, not  
249 overlapping with aIPS;
- 250 • *Posterior intraparietal sulcus (pIPS)*: on the posterior segment of the intraparietal sulcus, not  
251 overlapping with mIPS;
- 252 • *Superior parietal lobule (SPL)*: the anterior portion of the superior parietal lobule, superior to the  
253 IPS and slightly posterior to the postcentral sulcus;
- 254 • *Supramarginal gyrus (SMG)*: the anterior portion of the supramarginal gyrus, slightly posterior to  
255 the postcentral sulcus and superior to the lateral sulcus;
- 256 • *Dorsolateral prefrontal cortex (dlPFC)*: on the anterior portion of the middle frontal gyrus, around  
257 Brodmann area (BA) 46 (Badre & D'Esposito, 2009);
- 258 • *Supplementary motor area (SMA)*: on the medial wall of the superior frontal gyrus, anterior to the  
259 medial end of the central sulcus, posterior to the vertical projection of the anterior commissure;

- 260 • *Presupplementary motor area (preSMA)*: on the anterior segment of the cingulate sulcus, slightly  
261 anterior to the vertical projection of the anterior commissure;
- 262 • *Posterior superior temporal gyrus (pSTG)*: the posterior portion of the superior temporal gyrus,  
263 inferior to the supramarginal gyrus;
- 264 • *Posterior middle temporal gyrus (pMTG)*: the posterior portion of the middle temporal gyrus;

265 Next, we projected these marked activation patches from the surface back to the volume. Within each of  
266 them, we looked for individual peak voxels coming from the single-subject GLM contrasts [Planning >  
267 Baseline], computed as described above. We defined individual ROIs, separately for each participant, as  
268 spheres (8 mm radius) centered around each individual peak voxel (for a summary of the Talairach  
269 coordinates of individual ROIs, see Table 1). To examine classification performance in regions that are not  
270 expected to show predictive power, we additionally included a non-brain control ROI outside the skull of  
271 the brain near the right frontal cortex (same size and shape as before, and identical location for all  
272 participants).

273 <<Table 1>>

274 *Multivariate pattern classification analysis.*

275 We ran both ROI- and searchlight-based MVPA using support-vector-machines (SVM) as implemented in  
276 LIBSVM (Chang & Lin, 2011). The ROI analysis served to test whether we could decode planned movements  
277 in the regions identified individually by the functional contrast [Planning > Baseline] as described above. In  
278 addition, to rule out that we missed potentially important regions in the ROI analysis, we carried out a  
279 whole-brain surface-based searchlight analysis (Oosterhof et al., 2011; see also *Further Observations* in the  
280 Discussion). For the MVPA we estimated beta weights using the same design matrices as in the univariate  
281 analysis, except for the following: since participants freely selected which movements to plan and execute  
282 in the Free-Choice condition, the number of trials per movement type in the Free-Choice condition was not  
283 fully balanced. To prevent classification on the basis of the number of trials instead of the spatial patterns  
284 of brain activity, we balanced the number of trials per movement type in the Free-Choice and the  
285 Instructed condition by levelling to the minimum number of repetitions in either condition within each run,  
286 and discarding the trials in excess (randomly selected among the total). Beta maps containing the mean of  
287 the beta estimates of the 3<sup>rd</sup> and 4<sup>th</sup> timepoint for each predictor of interest (13, see *Univariate analysis*),  
288 individual spherical ROI (133 voxels) and run (10) were created for each participant. These maps were then  
289 z-transformed and normalized into multivoxel patterns of *t*-values (beta estimates divided by their standard  
290 error) that we used as input for the classifier. This procedure resulted in 10 multivoxel patterns of *t*-values  
291 per planning condition (one per experimental run). Classification accuracies were computed using a *leave-*  
292 *one-run-out* cross-validation method, i.e. the classifier was trained using data from 9 patterns and tested  
293 on the data from the remaining pattern. Note that while for the within-condition decoding all 10 patterns

294 came from the same condition, the classifier was trained with 9 patterns from one planning condition (e.g.  
295 Free-Choice) and tested on one pattern from the other planning condition (e.g. Instructed) for the cross-  
296 condition decoding. Training and testing was repeated for 10 iterations, using all possible combinations of  
297 train and test patterns. The average across these 10 iterations constituted the mean decoding accuracy per  
298 participant and ROI.

299 To decode upcoming hand movements from preparatory brain activity patterns, multiple binary  
300 classifiers were trained to discriminate between two movements within each of the three possible pairs of  
301 movements (i.e. precision grip vs power grip, precision grip vs touch, and power grip vs touch) during the  
302 Planning phase, separately for the Instructed and the Free-Choice condition. Classification accuracies from  
303 the three binary classifiers were successively combined to produce an average accuracy per ROI.

304 To test for representations of planned movement types independent of the planning condition, we  
305 carried out cross-condition decoding, i.e. training the classifier on discriminating movement pairs in one  
306 condition (e.g. precision grip vs power grip in the Instructed condition) and testing the performance of the  
307 classifier to distinguish between the same pair of movements in the other planning condition (e.g. precision  
308 grip vs power grip in the Free-Choice condition), and vice versa. As before, the mean of the three pairwise  
309 comparisons was computed to produce one accuracy score per ROI. Results from the two cross-condition  
310 decoding analyses (i.e. train on Instructed condition, test on Free-Choice condition, and vice versa) were  
311 also averaged. Finally, we carried out the same within-condition decoding analysis described above for the  
312 Execution phase, but, given that no differences were expected after the movement had started, we  
313 collapsed across planning conditions.

314 To assess statistical significance of the decoding accuracy, we entered the individual ( $N = 18$ )  
315 classification accuracies (averaged across the three pairwise comparisons) into two-tailed one-sample  $t$ -  
316 tests across participants against chance decoding (50%), separately for each ROI. Furthermore, to directly  
317 compare our main conditions of interest we performed post-hoc two-tailed paired samples  $t$ -tests between  
318 planning conditions for each ROI. Statistical results were corrected for multiple comparisons (number of  
319 ROIs  $\times$  number of tests) using the False-Discovery-Rate (FDR) method (Benjamini & Yekutieli, 2001).

320

321 *Brain segmentation, mesh reconstruction, and cortex-based alignment (CBA).* To create high quality 3D  
322 brain reconstructions, we gathered, when available, multiple anatomical scans from each participant  
323 collected in different experiments carried out at the Center for Mind/ Brain Sciences, which we aligned and  
324 averaged (min: 1, max: 13 scans). Individual surface meshes for each hemisphere were reconstructed along  
325 the border between grey and white matter. Next, individual reconstructions of each hemisphere were used  
326 to generate individual spherical surfaces for each participant that were then morphed to a template surface  
327 (a standard sphere). A coarse-to-fine moving target approach with four coarse-to-fine levels of smoothing  
328 was then used to extract multiscale surface curvature maps that reflect the gyral and sulcal folding patterns

329 (Fischl et al., 1999; Goebel et al., 2006). This information allowed us to align the individual standardized  
330 spherical surfaces of all participants to a group-averaged spherical surface. Transformation matrices  
331 resulting from the cortex-based alignment of individual spherical surfaces to the group-averaged spherical  
332 surface were then used to align individual functional maps before entering group statistics. Finally, using  
333 the curvature maps from CBA, we combined (i.e. averaged) the individual reconstructions of folded  
334 surfaces of all participants (N = 18) to create one group mesh for each hemisphere. Group-averaged left  
335 and right hemisphere meshes were used to display statistical maps coming from both uni- and multivariate  
336 group-analyses.

337

338 *Surface-based Searchlight SVM-MVPA.* The spherical searchlight (8 mm radius) was restricted to the surface  
339 by only including voxels from -1 to 3 mm along the grey/white matter boundary. Decoding procedures  
340 were very similar to the ones used for the ROI-based MVPA. For each hemisphere, we first created mesh-  
341 time-courses (MTCs) from the volume-time-courses (VTCs). Next, we used MTCs to generate whole-brain *t*-  
342 maps (20 per participant: 2 hemispheres x 10 runs), and finally we ran pairwise classifications on the *t*-maps  
343 as described above. Decoding results of the spherical searchlight were assigned to the central voxel.  
344 Individual surface accuracy maps were projected onto the group-averaged cortical surface mesh (see *Brain*  
345 *segmentation, mesh reconstruction, and cortex-based alignment*) and then anatomically aligned using the  
346 transformation parameters derived from cortex-based alignment. We successively performed a two-tailed  
347 one-sample *t*-test across individual cortical maps to identify vertices where classification was significantly  
348 greater than chance (50%). Statistical *t*-maps were thresholded at  $p < 0.01$  and corrected for multiple  
349 comparisons ( $p < 0.05$ ) using a cluster-size algorithm (Forman et al., 1995) based on Monte Carlo  
350 simulations (1000 iterations) as implemented in Brain Voyager 2.8.0. For each hemisphere, we generated *t*-  
351 maps and decoding accuracy maps separately for the Instructed condition, the Free-Choice condition, and  
352 across planning conditions.

353

## 354 **RESULTS**

### 355 **Behavioral results**

356 *Reaction times (RTs).* Participants responded slightly faster in the Instructed [602.12 ± 18.67 ms] compared  
357 to the Free-Choice condition [605.51 ± 18.65 ms;  $F(1,17) = 8.37, p < 0.01$ ]. However, RTs did not differ  
358 between movement types [ $F(2,34) = 0.42, p < 0.65$ ], and the interaction between planning condition and  
359 movement type was not significant [ $F(2,34) = 2.66, p < 0.08$ ].

360 *Error rates (ERs).* Participants were generally accurate in performing the delayed-movement task. Overall  
361 error rates were very low: 2.15% of all the trials in the Instructed condition, and 0.54% in the Free-Choice  
362 condition. The fact that error rates were lower in the Free-Choice compared to the Instructed condition  
363 was expected given that, while errors in the Free-Choice condition only concerned kinematics, timing, or

364 hand preshaping of the movements, errors in the Instructed condition also included executing a movement  
365 that was different from the instructed movement type.

366

367 *Shannon's Entropy in Free-Choice trials.* To examine whether the movements selected in successive trials  
368 followed a regular pattern, we calculated a measure of randomness for movement selection in Free-Choice  
369 trials, defined as Shannon's Entropy index (Shannon, 1948; see *Materials and methods*). A low entropy  
370 index ( $0 < H < 1$ ) indicates that one of the outcomes was chosen more often than others, or that the  
371 participant used a stereotyped transition pattern (e.g. 1 2 3, 1 2 3, etc.). By contrast, a high entropy index  
372 ( $H > 1.5$ ) indicates that it is very hard to predict the next outcome on the basis of the previous outcomes. In  
373 our study, the mean entropy index per participant was 1.53, which is close to the maximum entropy level  
374 for three alternatives ( $H = 1.584$ ). This analysis indicates that participants did not choose movements in a  
375 systematic, predictable way. As an example, this is a sequence chosen in the two consecutive blocks of one  
376 run by a representative participant: 2,1,2,3,2,2,1,1,3 – 2,1,2,3,2,3,1,2,2 (1 = precision grip, PRG; 2 = power  
377 grip, PWG; 3 = touch, TCH).

378

### 379 **Univariate RFX-GLM results**

380 To identify brain regions preferentially recruited during movement planning, we carried out a univariate  
381 random effects general linear model (RFX-GLM) contrast [Planning > Baseline] (Fig. 2A). Note that this  
382 contrast is unbiased with respect to comparisons between the Instructed and Free-Choice Planning  
383 condition, or between different movement types. The resulting statistical map was used to define 16  
384 group-ROIs: left primary motor cortex (L-M1); left dorsal and ventral premotor cortex (L-PMd, and L-PMv,  
385 respectively); left anterior, middle and posterior intraparietal sulcus (L-aIPS, L-mIPS, and L-pIPS,  
386 respectively); left superior parietal lobule (L-SPL); left supramarginal gyrus (L-SMG); left dorsolateral  
387 prefrontal cortex (L-dlPFC); left supplementary motor area (L-SMA); left pre-supplementary motor area (L-  
388 preSMA); right posterior intraparietal sulcus (R-pIPS); right posterior superior temporal gyrus (R-pSTG);  
389 right posterior middle temporal gyrus (R-pMTG); right supplementary motor area (R-SMA); and right pre-  
390 supplementary motor area (R-preSMA; for details on the definition of individual ROIs, see the section  
391 *Univariate analysis (GLM) and ROI definition* and Table 1). Additionally, we contrasted the Planning phase  
392 against the Baseline separately for the two planning conditions ([Planning Instructed > Baseline]; [Planning  
393 Free-Choice > Baseline], Fig. 2B). Overall, the statistical maps for the Instructed and Free-Choice planning  
394 condition looked very similar, in particular in the left hemisphere, and the direct comparison [Planning  
395 Instructed > Planning Free-Choice] did not reveal any significant univariate effects.

396

397

<< Figure 2 >>

398

399 **Multivariate results**

400 *ROI-based MVPA.* In the ROI-based MVPA we tested whether upcoming movements could be decoded on  
401 the basis of patterns of preparatory brain activity within regions recruited during movement planning. To  
402 this end, for each ROI and planning condition we ran two-tailed one-sample *t*-tests (FDR corrected for  
403 multiple comparisons) on the mean decoding accuracy across participants ( $N = 18$ ) against chance (50%).  
404 Figure 3 shows the mean classification accuracy in each ROI for averaged pairwise comparisons of  
405 movement types in four types of ROIs: (1) During the Planning phase, i.e. before any movement occurred,  
406 we found significant decoding of movement type both within (red and blue bars) and across (yellow bars)  
407 planning conditions in L-mIPS, L-pIPS, L-PMd, L-SPL, L-aIPS and L-M1, suggesting abstract representations of  
408 planned movements that generalize across planning condition (i.e. Instructed vs Free-Choice; Fig. 3A). (2)  
409 In R-pIPS, L-dIPFC, R-pSTG, L-PMv and R-pMTG we were able to predict upcoming movements for the Free-  
410 Choice planning condition, but not for the Instructed planning condition (Fig. 3B). In L-SMG we found a  
411 similar trend ( $p = 0.044$ ) that did not survive FDR correction for multiple comparisons. (3) In L-SMA we  
412 obtained above chance decoding for the Instructed, but not for the Free-Choice planning condition (Fig.  
413 3C). R-SMA ( $p = 0.018$ ), L-preSMA ( $p = 0.033$ ) and R-preSMA ( $p = 0.026$ ) showed trends in the same  
414 direction that did not pass FDR correction. (4) As expected, decoding of movement type was not possible  
415 (i.e. chance performance for all experimental conditions) in the non-brain control region outside the brain  
416 (Fig. 3D).

417 To further examine the nature of our effects, we performed post-hoc two-tailed paired samples *t*-tests on  
418 the mean decoding accuracy between the two planning conditions for each ROI. After FDR correction for  
419 multiple comparisons ( $q < 0.05$ ), these tests revealed a significant effect in L-PMv ( $t(17) = -4.44$ ,  $p = 0.0004$ ),  
420 indicating that decoding was significantly higher for Free-Choice compared to Instructed planning in this  
421 region. Post-hoc comparisons that did not survive FDR correction for multiple comparisons include R-pIPS  
422 ( $p = 0.016$ ), L-dIPFC ( $p = 0.027$ ), R-pSTG ( $p = 0.042$ ) and R-pMTG ( $p = 0.045$ ).

423 Finally, during the Execution phase (Fig. 3, green bars), we were able to decode upcoming movements in all  
424 the ROIs, with the exception of R-pSTG (trend at  $p = 0.043$ ), R-preSMA ( $p = 0.063$ ) and the non-brain control  
425 region. Not surprisingly, we observed the highest decoding accuracy during the execution phase in the left  
426 (contralateral) primary motor cortex (L-M1), followed by the left aIPS.

427 << Figure 3 >>

428 *Searchlight-based MVPA.* To identify additional regions beyond our ROIs that potentially represent  
429 information about upcoming movements, we conducted a whole-brain searchlight-based MVPA on the  
430 surface (Fig. 4, Fig. 5). Figure 4 shows the performance of the classifier across the two planning conditions  
431 superimposed on the group-averaged inflated surface mesh. The cross-condition decoding *t*-map (Fig. 4A)  
432 revealed significant clusters in left orbitofrontal (L-OFC) and fronto-polar cortex (L-FP), L-dIPFC, posterior  
433 dorsal L-SMA, L-PMd, left anterior superior temporal sulcus (L-aSTS), L-IPS, inferior L-SPL, L-pSTG, L-SMG,

434 left angular gyrus (L-AnG) and the left precuneus (L-preCu). In the right hemisphere, this analysis revealed  
435 significant clusters in R-FP, R-PMd, R-SPL, right superior parieto-occipital cortex (R-SPOC), R-pSTG, R-MTG  
436 and right lateral occipital gyrus (R-LOG).

437 Figure 5A shows the within-condition-decoding  $t$ -maps with cluster-size correction ( $p = 0.05$ ) for  
438 multiple comparisons (red, Instructed; blue, Free-Choice) and their overlap (purple). Overall, significant  
439 clusters for Instructed and Free-Choice Planning appeared in neighboring but mostly non-overlapping  
440 locations (except for the left anterior fronto-medial cortex, bilateral superior dIPFC and pSPL), and  
441 generally more widespread for the Free-Choice in comparison to the Instructed condition, especially in  
442 frontal (FP, dIPFC, PMd) and parietal (IPS, pIPL, pSPL) areas. For the Free-Choice planning condition we  
443 obtained significant clusters in the left hemisphere in the anterior fronto-medial cortex and L-OFC, L-FP, L-  
444 dIPFC, L-PMv, L-PMd, L-aIPS, L-pSPL, L-SPOC, L-AnG. In the right hemisphere, this analysis revealed  
445 significant clusters in R-FP, superior R-dIPFC, R-aIPS, R-SMG, R-pSTG, R-pIPS, the right posterior inferior  
446 parietal lobule (R-pIPL), R-pSPL, R-SPOC, and, medially, the right cuneus (R-Cu) and R-preCu. For the  
447 Instructed planning condition we obtained significant clusters in the left hemisphere in the superior L-  
448 dIPFC, the anterior fronto-medial cortex (slightly anterior to L-SMA and superior to L-preSMA), L-PMd, L-  
449 SMG, L-pSPL, and L-LOG. For the right hemisphere, we obtained significant clusters in the superior R-dIPFC,  
450 the anterior R-SPL (right above R-aIPS), R-MTG (extending to the superior temporal sulcus), R-pSPL and R-  
451 SPOC. When using a more conservative threshold of  $p = 0.001$  (not shown here), only clusters in L-dIPFC, L-  
452 PMd, L-IPS, for the cross-condition decoding, and in bilateral dIPFC, pSPL, L-aIPS, and R-pIPS for the Free-  
453 Choice planning condition survived (i.e. no clusters for Instructed planning condition).

454 Figures 4B and 5B illustrate mean decoding accuracies for the cross-condition (Fig. 4B) and within-  
455 condition (Fig. 5B) decoding. These figures show both significant and sub-threshold clusters of decoding  
456 accuracy to complement the information present in the searchlight  $t$ -maps. Although we observed slight  
457 discrepancies between the ROI-based and searchlight-based MVPA results in some regions (L-M1, L-aIPS, L-  
458 mIPS, L-SMG, R-pMTG, R-pSTG), overall searchlight results appear to be largely in line with ROI results in  
459 several frontal (L-dIPFC, L-PMd, L-PMv, bilateral SMA and preSMA) and parietal (L-pIPS, R-pIPS, L-SPL)  
460 regions (for a comparison of the two MVPA approaches see section *Further Observations* in the Discussion).

461 << Figure 4 >>

462 << Figure 5 >>

## 463 **DISCUSSION**

464 Frontal and parietal regions recruited during movement planning encode information about upcoming  
465 movements (Andersen & Buneo, 2002; Cisek & Kalaska, 2005; Cui & Andersen, 2007). Here we aimed to  
466 distinguish between areas representing abstract movement plans, areas involved in movement selection,  
467 and areas involved in the mapping between arbitrary sensory cues and the corresponding responses. We  
468 obtained three key results (summarized in Fig. 6): (1) contralateral (i.e. left) SPL and IPS, PMd and M1

469 discriminate between planned movements irrespective of the planning condition (i.e. both within and  
470 across internally- and externally-driven movements); (2) contralateral (i.e. left) PMv, dIPFC, SMG and  
471 ipsilateral (i.e. right) pIPS, pSTG, and pMTG encode internally-driven but not externally-driven movement  
472 plans. (3) Bilateral SMA, possibly supported by pre-SMA, encodes the processing of externally-driven  
473 movement plans.

474

#### 475 **Areas representing abstract movement plans**

476 We obtained significant within-condition decoding of movement plans for both planning conditions, as well  
477 as significant cross-condition decoding, in the left (i.e. contralateral to the moving limb) SPL, pIPS, mIPS,  
478 aIPS, PMd and M1 (Fig. 3A, Fig. 6). Our results are in line with studies showing that premotor regions are  
479 sensitive to arbitrary instructing cues (i.e. which movement to perform, or which effector to use; Hoshi  
480 & Tanji, 2000, 2006, 2007), while also participating in action selection, when movements are freely chosen  
481 (Beudel & de Jong, 2009; Cisek & Kalaska, 2005; Klaes et al., 2011; Pesaran et al., 2008). Our results thus  
482 show that contralateral parieto-frontal regions represent abstract movement plans that are invariant to the  
483 way these are generated rather than being tied to simple stimulus-response mapping (Hartstra et al., 2011,  
484 2012) or movement decisions.

485 Movement plans can be abstract in a number of different ways. For instance, Gallivan et al. (2013a,  
486 2013b) observed that bilateral posterior parietal cortex (PPC), PMd, posterior fusiform sulcus (pFs) and  
487 fusiform body area (FBA) contain representations of upcoming movements that generalize across the  
488 effector (left vs right hand). These studies provide further evidence for abstract representations of  
489 movement plans in frontal, parietal and ventral stream areas.

490 During movement execution, aIPS and M1 have been shown to represent handwriting movements  
491 generalizing across letter scale (Kadmon Harpaz et al., 2014). During movement observation, a number of  
492 recent studies revealed abstract action representations that generalize across viewpoint and modalities  
493 (Oosterhof et al., 2012a), and the object on which these actions are performed (Wurm & Lingnau, 2015;  
494 Wurm et al., in press), in aIPS and lateral occipitotemporal cortex (LOTc). Further research is required to  
495 determine to which degree abstract movement representations are shared across planning, observation,  
496 and execution.

497

#### 498 **Areas involved in action selection**

499 We were able to decode upcoming movements in the Free-Choice, but not in the Instructed condition in  
500 contralateral (left) PMv, dIPFC, SMG and ipsilateral (right) pIPS, pSTG, and pMTG (Fig. 3B, Fig. 6). The  
501 dorsolateral pathway has been historically associated with grasping movements (Jeannerod et al., 1995;  
502 Luppino et al., 1999; for a recent review see Turella & Lingnau, 2014). Our results extend these findings by  
503 revealing areas preferentially representing the selection rather than the planning of movements.



504 In contrast to studies that found significant decoding for instructed movements in PMv (Gallivan et  
505 al., 2011a, 2013a), we were able to decode upcoming movements in PMv for internally-driven but not for  
506 externally-driven movements, suggesting a more prominent role in action selection (i.e. deciding which  
507 movement to perform). It is possible that these inconsistencies are due to methodological differences. As  
508 an example, in contrast to the studies by Gallivan et al. (2011a, 2013a), participants in the current study  
509 neither saw the object nor their own hand throughout the experiment. Likewise, our planning phase was  
510 substantially shorter than the planning phase used by Gallivan et al. (2011a, 2013a). It is therefore possible  
511 that PMv represents both internally- and externally-triggered movement plans, depending on the  
512 availability of sensory cues and/ or time for movement planning.

513 We were able to decode internally-triggered movement plans in pMTG, a portion of the LOTC. LOTC  
514 is recruited during the processing of a variety of visual stimuli, e.g. basic and biological motion, tools, body  
515 parts and actions, but also has been implicated to host action concepts (for a recent review, see Lingnau &  
516 Downing, 2015). In addition, and perhaps more surprising, LOTC has been demonstrated to be recruited  
517 during the planning and control of actions (Astafiev et al., 2004; Kühn et al., 2011; Johnson-Frey et al.,  
518 2005; Gallivan et al., 2013b, 2015; Kilintari et al., 2014; Verhagen et al., 2008). Integrating various kinds of  
519 information from the dorsal (e.g. visuo-spatial, motoric) and the ventral stream (e.g. semantics), LOTC  
520 might be an optimal site of convergence to create a link between perceiving, understanding and interacting  
521 with the environment (Lingnau & Downing, 2015). Moreover, LOTC and the dorsal stream might exchange  
522 information about upcoming movements and/ or anticipated sensory consequences of selected actions  
523 (Kühn et al., 2011; Verhagen et al., 2008; Gallivan, 2014; Lingnau & Downing, 2015). Finally, some studies  
524 suggest that, in contexts that lack visual feedback, occipito-temporal regions could play a role in motor  
525 imagery, dynamically updating representations of the moving limbs (Astafiev et al., 2004; Kühn et al., 2011;  
526 but see Orlov et al., 2010).

527

#### 528 **Areas involved in stimulus-response associations**

529 We were able to decode externally-triggered movement plans in left SMA, with a similar trend in the right  
530 SMA and left preSMA (Fig. 3C, Fig. 5A), in agreement with previous studies (Hoshi & Tanji, 2004; Hartstra et  
531 al., 2012; Mars et al., 2008; Gallivan et al., 2011a, 2011b, 2013a). This suggests a role for the fronto-median  
532 cortex in stimulus-response mapping, possibly in a broader network that includes also posterior parietal  
533 and premotor regions (Figure 5). However, other studies have also linked SMA activity to voluntary action  
534 selection (Lau et al., 2004; Zhang et al., 2012, 2013) or self-initiated movements (Cunnington et al., 2002,  
535 2003; Fried et al., 2011). Further work will be required to define the specific role of the SMA and preSMA,  
536 and possibly also posterior parietal and premotor regions, in stimulus-response mapping and movement  
537 planning.

538

539 **Further observations**

540 The univariate contrast [Planning > Baseline] revealed a more widespread recruitment of the contralateral  
541 in comparison to the ipsilateral hemisphere (Fig. 2), whereas the searchlight MVPA revealed significant  
542 clusters in both hemispheres (Fig. 4, 5). It thus appears that, despite weak activation, the hemisphere  
543 ipsilateral to the moving limb (in our study: the right hemisphere) also contains information about planned  
544 movements (see also Gallivan et al., 2013a; Leoné et al., 2014). This apparent inconsistency is likely due to  
545 the fact that MVPA relies on differences between activation patterns that can occur in the absence of  
546 amplitude differences (e.g Haxby et al., 2012; Kriegeskorte et al., 2006).

547 We found significant cross-condition decoding in regions that only show significant within-condition  
548 decoding for one of the two planning conditions (Free-Choice: R-pSTG, R-MTG; Instructed: L-SMA; Fig. 3). At  
549 first glance, this result might look implausible: if a region codes movement plans independent of the task,  
550 then it should also reveal decoding in both tasks alone. There are, however, theoretical reasons that can  
551 explain this pattern of results. If condition A tends to evoke more consistent patterns in comparison to  
552 condition B, condition A might improve cross-condition decoding. If condition A is used for the training  
553 dataset, the classifier can more easily learn to distinguish the patterns. Likewise, if condition A is used for  
554 the testing dataset, even if the classifier was trained on condition B, it is more likely to guess correctly. In  
555 other words, training on more consistent patterns and testing on less consistent patterns (or vice versa)  
556 would produce better results than just training and testing within the same inconsistent pattern (see also  
557 Oosterhof et al., 2012b).

558 While the ROI- and the searchlight-based MVPA overall reveal converging results, the ROI analysis  
559 tended to be more sensitive than the searchlight analysis, in line with previous studies (Oosterhof et al.,  
560 2012b; Wurm & Lingnau, 2015). This is likely due to methodological differences between the two  
561 approaches (see also Etzel et al., 2013). In particular, the use of individual ROIs is less affected by individual  
562 differences in functional brain topography. By contrast, the searchlight approach is not limited to ROIs  
563 defined a priori, but requires stricter criteria to produce significant results: first, the exact same voxels in  
564 group space have to show significant decoding in the majority of participants. Second, given the number of  
565 voxels in the brain, correcting for multiple comparisons is a much harder problem for searchlight-based  
566 MVPA. Given the pros and cons of both approaches, we present both analyses to provide the reader with a  
567 more complete picture of the results.

568

569 **Conclusions**

570 Our results extend the existing literature on movement planning, distinguishing between regions containing  
571 abstract movement plans that are invariant to the way these were generated (externally- vs internally-  
572 driven), areas involved in movement selection, and areas containing movement plans for instructed  
573 movements.

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759 **FIGURE CAPTIONS**

760 **Figure 1.** Experimental question, design, timing and setup. **A.** Schematic representation of the research  
761 question: is it possible to distinguish between areas representing externally-triggered (instructed)  
762 movement plans (red), internally-triggered (freely chosen) movement plans (blue) and abstract movement  
763 plans that are invariant to the way these movement plans are generated (purple)? **B.** 2x3 mixed factorial  
764 design: Planning condition (Instructed, Free-Choice), blocked, and Movement type (precision grip, PRG: two  
765 fingers only, index and thumb; power grip, PWG: whole hand open; touch, TCH: hand closed in a fist,  
766 without hand preshaping), randomized. **C.** Example trial with timing (Instructed block, PRG). Each trial  
767 began with participants fixating a dot (Baseline) for a variable amount of time randomly selected from a  
768 geometric distribution ( $p = 0.3$ , 2000 - 6000 ms). This interval was followed by a color fixation cross (500  
769 ms) either instructing which movement to plan (Instructed blocks), or indicating to freely select one of the  
770 movements (Free-Choice blocks). The Planning phase consisted of a jittered ISI (independently chosen  
771 from the same geometric distribution). After this delay, an auditory cue (100 ms) provided the GO-signal to  
772 start the movement (Execution phase, 2500 ms). In the Instructed condition the color of the fixation cross  
773 corresponded to one of the three movements. In the Free-Choice condition the cue always had the same,  
774 non-informative, color (in this example, blue). **D.** Lateral view of a participant with the right hand at the  
775 home position. The central wooden target object on which the reach-to-grasp movements were performed  
776 was mounted on a plexiglas workspace positioned above the waist of the participant. The size of the small  
777 and large wooden cuboids were 2x2x1 and 7x7x2 cm, respectively. Participants saw the screen through a  
778 mirror attached to the head coil (line of sight illustrated by black dashed line). This setup ensured that  
779 participants neither saw the target object nor their own movements.

780

781 **Figure 2.** Univariate RFX-GLM analysis. **A.** The univariate contrast [Planning > Baseline] (collapsing across  
782 planning conditions) was used to identify ROIs preferentially involved in movement planning. The resulting  
783 statistical RFX group-map (N = 18) was corrected for multiple comparisons using a false discovery rate  
784  $q(\text{FDR}) < 0.05$  and projected on the group-averaged inflated surface mesh for visualization. Individual ROIs  
785 were defined as spheres (8 mm radius) around individual peak voxels resulting from single-subject  
786 statistical maps (black circles represent an example of the individual spherical ROIs; for additional details,  
787 see Materials and Methods section and Table 1). **B.** Univariate contrast [Planning > Baseline], separately for  
788 each Planning condition ([Planning Instructed > Baseline], red; [Planning Free-Choice > Baseline], blue),  
789 projected on the same group-averaged inflated surface mesh. Purple areas denote the overlap between  
790 the two statistical group maps.

791

792 **Figure 3.** ROI-based MVPA. Mean percentage decoding accuracies for movement type resulting from  
793 multiple binary classifiers. SVM classification accuracies for the three possible discriminations between

794 movement pairs were averaged to produce a unique score per ROI and planning condition. Red bars,  
795 Planning Instructed; blue bars, Planning Free-Choice; yellow bars, Planning cross-condition (see Methods);  
796 green bars, Execution (collapsing across Planning conditions). Statistical significance was assessed via one-  
797 sample *t*-tests (two-tailed) against 50% chance. Results were FDR-corrected for multiple comparisons  
798 (number of ROIs x number of tests). Significance levels: one black asterisk, uncorrected  $p < 0.05$ ; two black  
799 asterisks, uncorrected  $p < 0.005$ ; one red asterisk, FDR corrected  $q < 0.05$ . **A.** Regions where we found both  
800 significant within- and cross-condition decoding. **B.** Regions where we observed significant effects (or  
801 trends) for the Free-Choice, but not for the Instructed Planning task. **C.** Regions where we observed  
802 significant effects (or trends) for the Instructed, but not for the Free-Choice Planning task. **D.** Control non-  
803 brain region outside the brain.

804

805 **Figure 4.** Searchlight SVM-MVPA: cross-condition decoding. The spherical searchlight (8 mm radius) was  
806 restricted to the surface (-1 to 3 mm). Decoding procedures were very similar to the ones used for the ROI-  
807 based MVPA (see Materials and Methods section). **A.** Group *t*-map (thresholded at  $p < 0.01$  and then  
808 cluster-size corrected) for the cross-condition decoding projected on the group-averaged surface mesh.  
809 White dashed lines indicate the outlines of the statistical map revealed by the univariate contrast [Planning  
810 > Baseline]. **B.** Group accuracy map (%) for cross-condition decoding.

811

812 **Figure 5.** Searchlight SVM-MVPA: within-condition decoding. **A.** Group *t*-maps (thresholded at  $p < 0.01$  and  
813 then cluster-size corrected), separately for each planning condition (red, Instructed; blue, Free-Choice),  
814 projected on the group-averaged surface mesh. **B.** Group decoding accuracy maps (%) separately for each  
815 planning condition (Planning Instructed, left; Planning Free-Choice, right). All other conventions are the  
816 same as in Fig. 4.

817

818 **Figure 6.** Summary of decoding results for the Planning phase. Circles superimposed on the group-averaged  
819 surface mesh represent examples of individual spherical ROIs color-coded according to the results of the  
820 ROI MVPA (significant cross-condition decoding, yellow; preferential decoding for Free-Choice planning,  
821 blue; preferential decoding for Instructed planning, red). White-shaded areas with dashed outlines indicate  
822 the statistical map revealed by the univariate contrast [Planning > Baseline].

823 **TABLES**

824 **Table 1.** TAL coordinates (x, y, z rounded mean and standard deviation across participants) of individual  
 825 peak voxels for the ROIs identified by the group contrast [Planning > Baseline].

<b>Region</b>	<b>x</b>	<b>y</b>	<b>z</b>	<b>SD x</b>	<b>SD y</b>	<b>SD z</b>
L-M1	-33	-25	50	2,7	2,7	2,4
L-PMd	-25	-11	48	3,1	3,3	4,0
L-PMv	-46	3	27	4,5	2,3	5,1
L-aIPS	-39	-34	39	3,5	3,6	2,2
L-mIPS	-35	-45	40	2,7	3,5	2,1
L-pIPS	-30	-57	42	2,5	2,8	2,8
L-SPL	-31	-51	54	2,9	5,5	2,9
L-SMG	-56	-28	29	2,3	5,0	4,8
L-dIPFC	-36	34	28	3,4	3,3	2,8
L-SMA	-7	-3	50	1,5	2,6	4,4
L-preSMA	-8	4	41	1,7	3,6	2,5
R-pIPS	30	-50	42	2,3	3,3	2,5
R-pSTG	53	-39	13	3,9	2,7	3,0
R-pMTG	51	-51	4	3,4	5,2	3,7
R-SMA	6	-4	51	2,3	3,1	2,8
R-preSMA	7	7	39	1,6	3,3	2,3
Out of brain	51	53	56	0	0	0

826 **Abbreviations:** L-M1, left primary motor cortex; L-PMd, left dorsal premotor cortex; L-PMv, left ventral premotor  
 827 cortex; L-aIPS, left anterior intraparietal sulcus; L-mIPS, left middle intraparietal sulcus; L-pIPS, left posterior  
 828 intraparietal sulcus; L-SPL, left superior parietal lobule; L-SMG, left supramarginal gyrus; L-dIPFC, left dorsolateral  
 829 prefrontal cortex; L-SMA, left supplementary motor area; L-preSMA, left pre-supplementary motor area; R-pIPS, right  
 830 posterior intraparietal sulcus; R-pSTG, right posterior superior temporal gyrus; R-pMTG, right posterior middle  
 831 temporal gyrus; R-SMA, right supplementary motor area; R-preSMA, right pre-supplementary motor area.