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## Distinct neural components of visually guided grasping during planning and execution

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Neural components of visually guided grasping

Title:

**Distinct neural components of visually guided grasping during planning and execution**

Abbreviated title:

Neural components of visually guided grasping

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Author contributions:

All authors conceived and designed the study. LKK collected the data. LKK, KS, and GM analyzed the data with guidance from JCC. LKK, GM, JCC and RWF wrote the manuscript.

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1 **Abstract**

2 Selecting suitable grasps on three-dimensional objects is a challenging visuomotor  
3 computation, which involves combining information about an object (e.g., its shape,  
4 size, and mass) with information about the actor's body (e.g., the optimal grasp  
5 aperture and hand posture for comfortable manipulation). Here we used functional  
6 magnetic resonance imaging to investigate brain networks associated with these  
7 distinct aspects during grasp planning and execution. Human participants  
8 of either sex viewed and then executed preselected grasps on L-shaped objects  
9 made of wood and/or brass. By leveraging a computational approach that accurately  
10 predicts human grasp locations, we selected grasp points that disentangled the role  
11 of multiple grasp-relevant factors: grasp axis, grasp size, and object mass.  
12 Representational Similarity Analysis revealed that grasp axis was encoded along  
13 dorsal-stream regions during grasp planning. Grasp size was first encoded in  
14 ventral-stream areas during grasp planning, then in premotor regions during grasp  
15 execution. Object mass was encoded in ventral-stream and (pre)motor regions only  
16 during grasp execution. Premotor regions further encoded visual predictions of grasp  
17 comfort, whereas the ventral stream encoded grasp comfort during execution,  
18 suggesting its involvement in haptic evaluation. These shifts in neural  
19 representations thus capture the sensorimotor transformations that allow humans to  
20 grasp objects.

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22 **Significance Statement**

23 Grasping requires integrating object properties with constraints on hand and arm  
24 postures. Using a computational approach that accurately predicts human grasp  
25 locations by combining such constraints, we selected grasps on objects that  
26 disentangled the relative contributions of object mass, grasp size, and grasp axis  
27 during grasp planning and execution in a neuroimaging study. Our findings reveal a  
28 greater role of dorsal-stream visuomotor areas during grasp planning, and  
29 surprisingly, increasing ventral stream engagement during execution. We propose  
30 that during planning, visuomotor representations initially encode grasp axis and size.  
31 Perceptual representations of object material properties become more relevant  
32 instead as the hand approaches the object and motor programs are refined with  
33 estimates of the grip forces required to successfully lift the object.

34

**35 Introduction**

36 Grasping is one of the most frequent and essential everyday actions performed by  
37 humans and other primates (Betti et al., 2021), yet planning effective grasps is  
38 computationally challenging. Successful grasping requires identifying object  
39 properties including shape, orientation and mass, and considering how these interact  
40 with the capabilities of our hands (Fabbri et al., 2016; Maiello et al., 2019, 2021;  
41 Klein, Maiello et al., 2020). Whether an object is large or small, heavy or light,  
42 determines how wide we open our hands to grasp it and how much force we apply to  
43 lift it (Johansson and Westling, 1988; Cesari and Newell, 1999). Such grasp-relevant  
44 object properties, including weight, mass distribution, and surface friction can often  
45 be inferred visually before initiating actions (Fleming, 2017; Klein et al., 2021).

46 A recent computational model accurately predicts precision-grip grasp locations on  
47 3D objects of varying shape and non-uniform mass (Klein, Maiello et al., 2020). The  
48 model combines multiple constraints related to properties of the object and the  
49 effector, such as the torque associated with different grasps and the actor's natural  
50 grasp axis. However, it remains unclear which brain networks are involved in  
51 computing specific grasping constraints. Moreover, it is unknown whether all  
52 constraints are estimated during grasp planning (i.e., before action initiation; Gallivan  
53 et al., 2013, 2019) or whether some aspects are computed during action execution,  
54 allowing the actor to refine grasp parameters on-line before or during contact with  
55 the object. Here, we ask how information gets combined to evaluate and then  
56 execute grasps. While many previous studies have investigated the effects of  
57 individual attributes, during either grasp planning or execution, here we consider how  
58 multiple factors combine, and compare both planning and execution.

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59 Previous studies show that grasp-relevant representations are distributed across  
60 ventral and dorsal visual processing streams. Shape is represented throughout both  
61 streams (Sereno et al., 2002; Orban et al., 2006; Konen and Kastner, 2008; Orban,  
62 2011), with dorsal representations emphasizing information required for grasp  
63 planning (Srivastava et al., 2009). For example, dorsomedial area V6A—located in  
64 human superior parieto-occipital cortex (SPOC)—is involved in selecting hand  
65 orientation given object shape (Fattori et al., 2004, 2009, 2010; Monaco et al., 2011).  
66 Visual representations of material properties—also crucial for grasping—have been  
67 identified predominantly in ventral regions such as lateral occipital cortex (LOC), the  
68 posterior fusiform sulcus (pFS), and parahippocampal place area (PPA; Cant and  
69 Goodale, 2011; Hiramatsu et al., 2011; Gallivan et al., 2014; Goda et al., 2014,  
70 2016). Brain regions that transform these disparate visual representations into  
71 appropriate motor codes include Anterior Intraparietal Sulcus (aIPS), Ventral  
72 Premotor Cortex (PMv), Dorsal Premotor Cortex (PMd), and primary motor cortex  
73 (M1). Primate neurophysiology suggests that PMv (primate Area F5) encodes grip  
74 configuration (Murata et al., 1997; Raos et al., 2006; Theys et al., 2012), while PMd  
75 (primate Area F2) encodes grip/wrist orientation (Raos et al., 2004). Both regions  
76 exhibit strong connections with aIPS, which could play a key role in linking visual  
77 representations—including those in ventral stream regions (Borra et al., 2008)—to  
78 motor commands sent to the hand through M1 (Murata et al., 2000; Janssen and  
79 Scherberger, 2015).

80 How information flows and is combined across this complex network of brain regions  
81 is far from understood. We therefore sought to identify cortical regions associated  
82 with distinct components of grasping and tested their relative importance during  
83 grasp planning and execution. To disentangle grasping constraints, we used our

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84 model (Maiello et al., 2021) to select grasps that placed different constraints in  
85 conflict. For example, a selected grasp could be near optimal in terms of the required  
86 hand axis, but sub-optimal in terms of grasp aperture. We then measured functional  
87 magnetic resonance imaging (fMRI) blood-oxygen-level-dependent (BOLD) activity,  
88 during planning and execution of these preselected grasps. Combining this model-  
89 guided approach with representational similarity analysis (RSA; Kriegeskorte, 2008)  
90 let us tease apart the relative contributions of object mass, grasp size, and grasp  
91 axis, at different stages of grasping.

92

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93 **Materials and Methods**

94 **Participants.** Analyses utilized data from 21 participants (13 female, mean [range]  
95 age: 25.5 [18-33]) recruited from the University of Western Ontario. Data from two  
96 additional participants were excluded due to excessive head motion. All participants  
97 had normal or corrected-to-normal vision and were fully right-handed as measured  
98 by the Edinburgh Handedness Inventory. Informed consent was given prior to the  
99 experiment. The study was approved by the Health Sciences Research Ethics Board  
100 at the University of Western Ontario and followed the principles in the 6<sup>th</sup> revision of  
101 the Declaration of Helsinki (2008). Participants were instructed on how to perform  
102 the experimental task before entering the MRI room, yet remained naïve with respect  
103 to the study's hypotheses. Participants were financially compensated at a rate of  
104 C\$25/hour.

105 **Setup.** A schematic of our setup is shown in **Figure 1A**. Each participant lay supine  
106 inside the MRI scanner with their head placed in a head coil tilted by  $\sim 30^\circ$  to allow  
107 direct viewing of real stimulus objects placed in front of them. Below the head we  
108 positioned the bottom 20 channels of a 32-channel head coil and we suspended a 4-  
109 channel flex coil via loc-line (Lockwood Products, Inc.) over the forehead. A black  
110 wooden platform, placed above a participant's hip, enabled the presentation of real  
111 objects that participants were required to grasp, lift, and set back down using their  
112 right hand. The platform's flat surface was tilted by  $\sim 15^\circ$  towards a participant in  
113 order to maximize comfort and visibility. Objects were placed on a black cardboard  
114 target ramp (**Figure 1A**: "Ramp", dimensions: 15 x 5 x 13 cm) on top of the platform  
115 that created a level surface which prevented objects from tipping over. The objects'  
116 exact placement was adjusted such that all required movements were possible and  
117 comfortable. Between trials, a participant's right hand rested on a button at a start

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118 position on the table's lower right side. The button monitored movement start and  
119 end times. A participant's upper right arm was strapped to their upper body and the  
120 MRI table using a hemi-cylindrical brace (not displayed in **Figure 1A**). This  
121 prevented shoulder and head movements, thus minimizing movement artefacts while  
122 enabling reach-to-grasp movements through elbow and wrist rotations. A small red  
123 LED fixation target was placed above and at a slightly closer depth location than the  
124 object to control for eye movements. Participants were required to maintain fixation  
125 on this target at all times during scanning. An MR-compatible camera was positioned  
126 on the left side of the head coil to record the participant's actions. Videos of the runs  
127 were screened offline and trials containing errors were excluded from further  
128 analyses. A total of 22 error trials were excluded, 18 of which occurred in one run  
129 where the participant erroneously grasped the objects during the planning phase.

130 Two bright LEDs illuminated the workplace for the duration of the planning and  
131 execution phases of each trial, one was mounted on the head coil and the other was  
132 taped to the ceiling of the bore. Another LED was taped to the outside of the bore  
133 and was only visible to the experimenter to cue the extraction and placement of the  
134 objects. The objects were kept on a table next to the MRI-scanner, on which three  
135 LEDs cued the experimenter on which object to place inside the scanner.  
136 Participants wore MR-safe headphones through which task instructions were relayed  
137 on every trial. The LEDs and headphones were controlled by a MATLAB script on a  
138 PC that interfaced with the MRI scanner. Triggers were received from the scanner at  
139 the start of every volume acquisition. All other lights in the MRI room were turned off  
140 and any other potential light sources and windows were covered so that no other  
141 light could illuminate the participant's workspace.

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142 **Stimuli.** Stimuli were three L-shaped objects of the same size, created from seven  
143 blocks (cubes of 2.5 cm side length). One object was constructed with seven cubes  
144 of beech wood (object weight: 67g), whereas the other two were both constructed of  
145 four brass and three wooden cubes (object weight: 557g). We performed pilot testing  
146 to ensure that the objects and their movements did not evoke artifacts related to the  
147 movement of masses within the scanner (Barry et al., 2010). Specifically, we placed  
148 a spherical MRI phantom (immobile mass) in the scanner and collected fMRI data  
149 while the experimenter placed and removed the objects, as they would in the actual  
150 experiment. Functional time courses were carefully examined to ensure that no  
151 artifacts were observed (such as spikes or abrupt changes in signal at the time of  
152 action, e.g., Culham, 2006; Singhal et al., 2013). The two identical wood-brass  
153 objects were positioned in two different orientations, one with the brass “arm”  
154 pointing up (see **Figure 1F**: “BrassUp”), the other with the brass arm lying down  
155 (“BrassDown”). In a slow event-related fMRI design, on each trial participants directly  
156 viewed, grasped, and lifted an object placed on a platform.

157 **Task.** Participants performed three distinct grasps per object, each grasp marked on  
158 the objects with coloured stickers during the experiment. The colours were clearly  
159 distinguishable inside the scanner and served to cue participants about which grasp  
160 to perform. Participants were instructed to perform three-digit grasps with their right  
161 hand, by placing the thumb in opposition to index and middle fingers. This grasp was  
162 similar to the precision grip grasps employed in our previous work (Maiello et al.,  
163 2019, 2021; Klein, Maiello et al., 2020; Klein et al., 2021), but ensured participants  
164 could apply sufficient grip force to lift all objects to a height of approximately 2 cm  
165 above the platform. Grasp contact locations for the index and thumb were selected in  
166 order to produce a set of uncorrelated—and thus linearly independent—

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167 representational dissimilarity matrices (RDMs) for the three grasp factors  
168 investigated: grasp axis, grasp size, and object mass. Specifically, grasps could be  
169 rotated 45° either clockwise or counter clockwise around the vertical axis, and could  
170 require small (2.5 cm) or large (7.5 cm) grip apertures. In pilot testing we further  
171 refined the positioning of the objects and grasps within the magnetic field of the MRI  
172 scanner to avoid the forming of eddy currents within the brass parts of the objects  
173 which could hinder participants from executing the grasps. The complete set of grasp  
174 conditions is shown in **Figure 1C**.

#### 175 **Experimental Design and Statistical Analysis**

176 **fMRI Experimental Procedure.** We employed a slow event-related fMRI design with  
177 trials spaced every 23-31 s. Participants underwent 4 experimental runs in which  
178 they performed each combination of 3 objects x 3 grasps twice per run (18 trials x  
179 run, 72 trials total) in a pseudorandom order to minimize trial order effects (van  
180 Polanen and Davare, 2015a; Maiello et al., 2018; van Polanen et al., 2020). The  
181 sequence of events occurring on each trial is schematized in **Figure 1B**. Prior to  
182 each trial, the experimenter was first cued on which object to place inside the  
183 scanner. The experimenter placed the object on the ramp. At trial onset, the  
184 illumination LEDs turned on and over the headphones the participant heard the  
185 instruction “plan”, immediately followed by the auditory cue specifying which grasp to  
186 execute. The auditory cue was “blue”, “green”, or “red”, which corresponded to  
187 coloured stickers marking the grasp locations on the objects. The duration of the  
188 planning phase of the task was randomly selected to be 6, 8, 10, or 12 s. During this  
189 time, the participant was required to hold still and mentally prepare to grasp the  
190 object at the cued location. Following previous research (Gallivan et al., 2014, 2015),  
191 we employed a variable delay between cue and movement onset to distinguish

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192 sustained planning-related neural activity from the movement-execution response  
193 accompanying action initiation. It is important to note that what we refer to with the  
194 term “action planning”, is a sustained action planning, pre-viewing phase in which  
195 participants are thinking about how to execute the movement and must thus access  
196 mental representations of the object and task. In this kind of delayed action task,  
197 previous work has demonstrated that dorsal-stream areas plan and maintain action  
198 goals (Singhal et al., 2013). We specifically do not mean the purely feedforward  
199 movement planning which occurs only a few hundred milliseconds prior to movement  
200 initiation (e.g., Westwood and Goodale, 2003), because it is unfeasible to investigate  
201 neural signals at this time scale though fMRI BOLD activity.

202 Once the planning phase ended, “lift” was played over headphones to cue the  
203 participant to execute the grasp. During the execution phase of the task, the  
204 participant had 7 s to reach, grasp, and lift the object straight up by approximately 2  
205 cm, place it back down on the target ramp, and return their hand to the start position.  
206 The illumination LEDs turned off, and the participant waited for a 10-12 s intertrial  
207 interval (ITI) for the next trial to begin. During the ITI the experimenter removed the  
208 object and placed the next one before the onset of the following trial. We note that  
209 we did not include a passive preview phase in our trial design, because we have  
210 repeatedly shown in previous studies that action intentions cannot be decoded from  
211 neural activity recorded during passive stimulus preview (Gallivan et al., 2011,  
212 2013b, 2013a).

213 Participants were instructed about the task, familiarized themselves with the objects,  
214 and practiced the grasps outside of the MRI room for about 5 minutes prior to the  
215 experiment. Once participants were strapped into the setup, they practiced all grasps  
216 again, thus ensuring that they could comfortably grasp each object.

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217 **Grasp Comfort Ratings.** At the end of the fMRI experiment, participants remained  
218 positioned in the scanner and performed a short rating task. Participants were asked  
219 to perform one more time each of the nine grasp conditions. For each grasp,  
220 participants verbally reported how comfortable the grasp was on a scale of 1-10 (1  
221 being highly uncomfortable and 10 being highly comfortable). Verbal ratings were  
222 manually recorded by the experimenter.

223 **Analyses.** Data analyses were conducted using Brain Voyager 20.0 (BV20) and  
224 21.4 (BV21.4) software packages (Brain Innovation, Maastricht, The Netherlands),  
225 as well as MATLAB version R2019b.

226 **fMRI data acquisition.** Imaging was performed using a 3-Tesla Siemens Prisma Fit  
227 MRI scanner at the Robarts Research Institute at the University of Western Ontario.  
228 Functional MRI volumes were acquired using a T2\*-weighted, single-shot, gradient-  
229 echo echo-planar imaging acquisition sequence. Functional scanning parameters  
230 were: time to repetition (TR) = 1000 ms; time to echo (TE) = 30 ms; field of view =  
231 210 x 210 mm in-plane; 48 axial 3-mm slices; voxel resolution = 3-mm isotropic; flip  
232 angle = 40°; and multi-band factor = 4. Anatomical scans were acquired using a T1-  
233 weighted MPRAGE sequence with parameters: TR = 2300 ms; field of view = 248 x  
234 256 mm in-plane, 176 sagittal 1-mm slices; flip angle = 8°; 1-mm isotropic voxels.

235 **fMRI data preprocessing.** Brain imaging data were preprocessed using the BV20  
236 Preprocessing Workflow. First, we performed Inhomogeneity Correction and  
237 extracted the brain from the skull. We then coregistered the functional images to the  
238 anatomical images, and normalized anatomical and functional data to Montreal  
239 Neurological Institute (MNI) space. Functional scans underwent motion correction  
240 and high-pass temporal filtering (to remove frequencies below 3 cycles/run). No slice  
241 scan time correction and no spatial smoothing were applied.

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242 **General linear model.** Data were further processed with a random-effects general  
243 linear model that included one predictor for each of the 18 conditions (3 grasp  
244 locations x 3 objects x 2 phases [planning vs. execution]) convolved with the default  
245 Brain Voyager “two-gamma” hemodynamic response function (Friston et al., 1998)  
246 and aligned to trial onset. As predictors of no interest, we included the 6 motion  
247 parameters (x, y, and z translations and rotations) resulting from the 3D motion  
248 correction.

249 **Definition of Regions of Interest.** We investigated a targeted range of regions of  
250 interest (ROIs). The locations of these ROIs are shown in **Figure 1H**; the criteria  
251 used to define the regions and their MNI coordinates are given in Table 1. ROIs were  
252 selected from the literature as regions most likely specialized in the components of  
253 visually guided grasping investigated in our study. These included primary visual  
254 cortex V1, areas LO, pFS, and PPA within the ventral visual stream  
255 (occipitotemporal cortex), areas SPOC, aIPS, PMv, PMd within the dorsal visual  
256 stream (occipitoparietal and premotor cortex), and primary sensorimotor cortex  
257 M1/S1.

258 Primary visual cortex (V1) was included because it represents the first stage of  
259 cortical visual processing upon which all subsequent visuomotor computations rely.  
260 Primary motor area M1 was included instead as the final stage of processing, where  
261 motor commands are generated and sent to the arm and hand. In our study,  
262 however, we refer to this ROI as primary motor and somatosensory cortex M1/S1,  
263 because our volumetric data do not allow us to distinguish between the two banks of  
264 the central sulcus along which motor and somatosensory regions lie.

265 We next selected regions believed to perform the sensorimotor transformations that  
266 link visual inputs to motor outputs. The dorsal visual stream is thought to be

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267 predominantly specialized for visually guided actions, whereas the ventral stream  
268 mostly specializes in visual object recognition (Goodale and Milner, 1992; Culham et  
269 al., 2003; Cavina-Pratesi et al., 2007; Vaziri-Pashkam and Xu, 2017). Nevertheless,  
270 significant crosstalk occurs between these streams (Budisavljevic et al., 2018), and  
271 visual representations of object material properties have been found predominantly  
272 in ventral regions. We therefore selected areas across both dorsal and ventral visual  
273 streams that would encode grasp axis, grasp size, and object mass.

274 We expected grasp axis could be encoded in dorsal stream regions SPOC (Fattori et  
275 al., 2004, 2009, 2010; Monaco et al., 2011), aIPS (Taubert et al., 2010), PMv  
276 (Murata et al., 1997; Raos et al., 2006; Theys et al., 2012), and PMd (Raos et al.,  
277 2004). We expected grasp size to be encoded in dorsal stream regions SPOC, aIPS  
278 (Monaco et al., 2015), PMd (Monaco et al., 2015), and PMv (Murata et al., 1997;  
279 Raos et al., 2006; Theys et al., 2012), and ventral stream region LO (Monaco et al.,  
280 2015). We expected visual estimates of object mass to be encoded in ventral stream  
281 regions LO, pFS, and PPA (Cant and Goodale, 2011; Hiramatsu et al., 2011;  
282 Gallivan et al., 2014; Goda et al., 2014, 2016). We further hypothesised that the  
283 network formed by aIPS, PMv, and PMd might play a role in linking ventral stream  
284 representations of object mass to the motor commands generated and sent to the  
285 hand through M1 (Murata et al., 2000; Borra et al., 2008; Davare et al., 2009, 2010,  
286 2011; Janssen and Scherberger, 2015; van Polanen and Davare, 2015b;  
287 Schwettmann et al., 2019; Schmid et al., 2021).

288 It should be noted that we do not expect the set of ROIs investigated here to be the  
289 exhaustive set of regions involved in visually-guided grasping. For example,  
290 subcortical regions are also likely to play a role (Nowak et al., 2007; Prodoehl et al.,  
291 2009; Cavina-Pratesi et al., 2018). However, cortical and subcortical structures

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292 require different imaging protocols (De Hollander et al., 2017; Miletic et al., 2020),  
293 and the small size and heterogeneity of subcortical structures also require different  
294 normalization, co-registration, and alignment techniques than those used in the  
295 cortex (e.g. Diedrichsen et al., 2010). Moreover, adding further ROIs would reduce  
296 statistical power when correcting for multiple comparisons. We thus chose to focus  
297 on a constrained set of cortical regions for which we had a-priori hypotheses  
298 regarding their involvement in the aspects of visually-guided grasping investigated  
299 here. Nevertheless, we hope that exploratory analyses on our open access data may  
300 guide future studies mapping out the distributed neural circuitry involved in visually-  
301 guided grasping.

302 **Figure 1H** shows our selected ROIs as volumes within the Colin27 template brain.  
303 To locate all left hemisphere ROIs (except V1) in a standardized fashion we  
304 searched the automated meta-analysis website *neurosynth.org* (Yarkoni et al., 2011)  
305 for key words (**Table 1**), which yielded volumetric statistical maps. Visual inspection  
306 of the maps allowed us to locate the ROIs we had pre-selected based on a  
307 combination of activation peaks, anatomical criteria, and expected location from the  
308 relevant literature. For example, aIPS was selected based on the hotspot for  
309 “grasping” nearest to the intersection of the intraparietal and postcentral sulci  
310 (Culham et al., 2003). Spherical ROIs of 15-mm diameter, centred on the peak voxel,  
311 were selected for all regions except V1. Because Neurosynth is based on a meta-  
312 analysis of published studies, search terms like “V1” would be biased to the typical  
313 retinotopic locations employed in the literature and likely skewed towards the foveal  
314 representation (whereas the objects and hand would have been viewed across a  
315 larger expanse within the lower visual field). As such, we defined V1 in the left  
316 hemisphere’s V1 using the (Wang et al., 2015) atlas, which mapped retinotopic

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317 cortex +/-  $\sim 15^\circ$  from the fovea. **Table 1** presents an overview of our ROI selection,  
318 where we list all our Neurosynth-extracted ROIs with their peak coordinates, search  
319 terms and download dates. We also share our ROIs (in MNI space) in the *nifti* format  
320 (doi upon acceptance).

321 **Representational Similarity Analysis.** The analysis of activation patterns within the  
322 selected ROIs was performed using multivoxel pattern analysis, specifically  
323 representational similarity analysis (RSA) (Kriegeskorte, 2008; Kriegeskorte et al.,  
324 2008). An activation pattern corresponded to the set of normalized  $\beta$ -weight  
325 estimates of the blood oxygenation level-dependent (BOLD) response of all voxels  
326 within a specific ROI for a specific condition. To construct representational  
327 dissimilarity matrices (RDMs) for each ROI, we computed the dissimilarity between  
328 activation patterns for each condition. Dissimilarity was defined as  $1-r$ , where  $r$  was  
329 the Pearson correlation coefficient. RDMs were computed separately from both  
330 grasp planning and grasp execution phases. These neural RDMs computed were  
331 then correlated to model RDMs (**Figure 1D,E,F**) to test whether neural  
332 representations encoded grasp axis, grasp size, and object mass. To estimate  
333 maximum correlation values expected in each region given the between-participant  
334 variability, we computed the upper and lower bounds of the noise ceiling. The upper  
335 bound of the noise ceiling was computed as the average correlation of each  
336 participant's RDMs with the average RDM in each ROI. The lower bound of the noise  
337 ceiling was computed by correlating each participant's RDMs with the average of the  
338 other participants' RDMs. All correlations were performed between upper triangular  
339 portions of the RDMs excluding the diagonal. We then used one-tailed Wilcoxon  
340 signed rank tests to determine whether these correlations were significantly  $>0$  within  
341 each ROI. We set statistical significance at  $p < .05$  and applied false discovery rate

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342 (FDR) correction for multiple comparisons following (Benjamini and Hochberg,  
343 1995).

344 To visualize the representational structure of the neural activity patterns within grasp  
345 planning and grasp execution phases, we first averaged RDMs across participants in  
346 each ROI and task phase. We then correlated average RDMs across ROIs within  
347 each phase and used hierarchical clustering and multidimensional scaling to  
348 visualize representational similarities across brain regions. We also correlated  
349 average RDMs across ROIs and across planning and execution phases. Statistically  
350 significant correlations ( $p < .05$  with Bonferroni correction) are shown also as  
351 topological connectivity plots (within-phase data) and as Sankey diagram (between-  
352 phase data).

353 **Grasp Comfort Ratings.** Grasp comfort ratings were analysed using simple t-tests  
354 to assess whether ratings varied across different grasp axes, grasp sizes, or object  
355 mass. The difference between ratings for each condition was then used to create  
356 grasp comfort RDMs for each participant. Grasp comfort RDMs were correlated to  
357 model RDMs to further test how strongly grasp comfort corresponded to grasp axis,  
358 grasp size, and object mass. To search for brain regions that might encode grasp  
359 comfort, the average grasp comfort RDM was correlated to neural RDMs following  
360 RSA as described above.

361 **Results**

362 Participants in a 3-Tesla MRI scanner were presented with physical 3D objects on  
363 which predefined grasp locations were shown (**Figure 1A**). On each trial,  
364 participants first planned how to grasp the objects (planning phase, **Figure 1B**) and  
365 then executed the grasps (execution phase). We designed objects and grasp  
366 locations to produce a set of nine distinct conditions (**Figure 1C**) that would  
367 differentiate three components of grasping: the grasp axis (i.e., orientation), the  
368 grasp size (i.e., the grip aperture), and object mass. By computing pairwise  
369 distances between all conditions for each of these grasp-relevant dimensions, we  
370 constructed one representational dissimilarity matrix (RDM) for each component  
371 (**Figure 1D-F**)—these were uncorrelated across conditions. In each brain region of  
372 interest (ROI) tested in the study (**Figure 1H**), brain-activity patterns elicited by each  
373 condition were compared to each other via Pearson correlation to construct brain  
374 RDMs. **Figure 1G** shows one such RDM computed from brain region PMv for one  
375 example participant during the planning phase. In this participant, this area appeared  
376 to strongly encode grasp axis.

377 **How grasp-relevant neural representations develop across the grasp network.**

378 **Figure 2A** shows average neural RDMs computed throughout the network of  
379 visuomotor brain regions we investigated. ROIs were selected from the literature as  
380 regions most likely specialized in the components of visually guided grasping  
381 investigated in our study. We included primary visual cortex, V1, as the first stage of  
382 cortical visual processing. Areas LOC, pFS, and PPA within the ventral visual stream  
383 (occipitotemporal cortex) were included as they are known to process visual shape  
384 and material appearance (Cant and Goodale, 2011; Hiramatsu et al., 2011; Gallivan  
385 et al., 2014; Goda et al., 2014, 2016), and could thus be involved in estimating object

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386 mass. Areas SPOC, aIPS, PMv, and PMd within the dorsal visual stream  
387 (occipitoparietal and premotor cortex) were included as they are thought to transform  
388 visual estimates of shape and orientation into motor representations (Janssen and  
389 Scherberger, 2015). Primary motor and somatosensory area (M1/S1, in the central  
390 sulcus) was included as the final stage of cortical sensorimotor processing. The  
391 patterns of correlations between model and neural RDMs across participants and  
392 ROIs (**Figure 2B-G**) reveal which information was encoded across these visuomotor  
393 regions during grasp planning and execution phases.

394 **Grasp axis encoding in visuomotor regions during grasp planning. Figure**  
395 **2B,C** shows that neural representations in V1 and ventral region LOC were  
396 significantly correlated with grasp axis during both grasp planning and execution  
397 phases. In contrast, representations in ventral areas pFS and PPA were never  
398 significantly correlated with grasp axis. Further, grasp axis was significantly  
399 correlated with neural representations across all dorsal areas (SPOC, aIPS, PMv,  
400 PMD), as well as M1/S1, but only during grasp planning. Dorsal and motor areas  
401 thus robustly encoded the orientation of the hand when preparing to grasp objects,  
402 suggesting that the hand-wrist axis was among the first components of the action  
403 computed across these regions.

404 **Grasp size was encoded across both visual streams during grasp planning**  
405 **and execution.** During the planning phase (**Figure 2D**), grasp size significantly  
406 correlated with neural representations in all ventral areas (LOC, pFS, PPA), and with  
407 representations in dorsal regions aIPS and PMd. During the execution phase  
408 (**Figure 2E**), grasp size remained significantly correlated with neural representations  
409 in ventral areas LOC and PPA, but not pFS. In the dorsal stream during the  
410 execution phase, grasp size remained significantly correlated with neural

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411 representations in PMd but not aIPS, and became significantly correlated with  
412 representations in PMv. Neural representations in early visual area V1 were  
413 significantly correlated with grasp size only in the execution phase, but not during  
414 planning. Thus, different ventral and dorsal areas encoded grasp size at different  
415 time points. These data suggest that ventral regions may have been initially involved  
416 in computing grasp size and might have relayed this information (e.g., through aIPS)  
417 to the premotor regions tasked with generating the motor codes to adjust the  
418 distance between fingertips during the execution phase. It is perhaps surprising to  
419 note that neural representations in M1/S1 were never significantly correlated with  
420 grasp size, given the well-established role of these regions in sensorimotor  
421 processing and motor control. These patterns may align however with findings from  
422 (Monaco et al., 2015), which suggest that M1/S1 are insensitive to object size, and  
423 could be related to work by Smeets and Brenner (Smeets and Brenner, 1999, 2001;  
424 Smeets et al., 2019), who propose that grip formation emerges from independently  
425 controlling the movements of the digits, rather than the size of the grip aperture.

426 **Object mass was encoded across dorsal and ventral streams and in motor**  
427 **areas, but only during grasp execution.** During the planning phase (**Figure 2F**),  
428 none of the investigated ROIs exhibited any activity that was significantly correlated  
429 with object mass. Conversely, during the execution phase (**Figure 2G**), object mass  
430 significantly correlated with representations in ventral areas pFS and PPA, dorsal  
431 areas aIPS and PMd, and sensorimotor area M1/S1. Object mass was thus encoded  
432 in the later stages of grasping. One possible interpretation is that this occurred when  
433 the hand was approaching the object and was preparing to apply appropriate forces  
434 at the fingertips. Alternatively, it could be due to sensory feedback about slippage  
435 once the object was lifted.

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436 **Representational similarities within the grasp network.** We took the RDMS  
437 generated for each of the nine ROIs (**Figure 2**) and correlated them with one another  
438 to reveal inter-ROI similarity relationships. **Figure 3** summarizes the resulting  
439 second-order similarity relationships, both within and between planning and  
440 execution phases.

441 We find that neural representations were significantly correlated across many  
442 selected ROIs during both grasp planning (**Figure 3A**) and execution (**Figure 3C**).  
443 Of particular note is that during the planning phase, dorsal regions tended to  
444 correlate more strongly with one another, while during the execution phase, ventral  
445 regions showed more correlated representations. This is revealed by visualising the  
446 inter-ROI similarities arranged topographically within a schematic brain (**Figure 3B**  
447 **and 3D**), with the darkness of connecting lines between ROIs proportional to the  
448 correlations between their corresponding RDMS.

449 During planning (**Figure 3B**), the strongest correlations were between M1/S1, PMd  
450 and aIPS; between V1 and SPOC; and to a lesser extent between SPOC and  
451 M1/S1. The structure of these representational similarities is shown also in the  
452 multidimensional scaling plot, where a gradient of information can be visualized from  
453 V1 through dorsal regions SPOC and aIPS towards motor regions PMd and M1/S1.  
454 In the execution phase (**Figure 3D**) the similarities among brain regions formed two  
455 main clusters. One cluster of visual regions was formed by V1, SPOC, and LOC. The  
456 second cluster comprised aIPS, premotor areas PMv and PMd, and M1/S1.  
457 Hierarchical clustering, multidimensional scaling, and topographical plots all highlight  
458 how these two clusters appeared to share representational content predominantly  
459 through ventral stream regions pFS and PPA.

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460 **Shared representations across planning and execution phases.** Neural  
461 representation patterns were also partly correlated across grasp planning and  
462 execution phases (**Figure 3E,F**). Notably, aIPS representations during the planning  
463 phase were significantly correlated with representational patterns in ventral (PPA),  
464 dorsal (SPOC, PMd), and sensorimotor (M1/S1) regions during the execution phase.  
465 This suggests that aIPS may play a key role in linking grasp planning to execution.  
466 Further, neural representation patterns in nearly all ROIs (except PMv) during the  
467 planning phase were correlated with representations in V1 during the execution  
468 phase, and representations in PFs, SPOC, PMd, and M1/S1 during action planning  
469 were correlated with LOC representations during action execution. We speculate that  
470 this might reflect mental simulation, prediction, and feedback mechanisms at play  
471 (see **Discussion**).

472 **Grasp comfort.** We recently demonstrated that humans can visually assess which  
473 grasp is best among competing options and can refine these judgements by  
474 executing competing grasps (Maiello et al., 2021). These visual predictions and  
475 haptic evaluations of grasp comfort were well captured by our multi-factorial model  
476 (Klein, Maiello et al., 2020), suggesting they may play a role in grasp selection. We  
477 thus wondered whether we could identify, within the grasp network investigated here,  
478 brain regions that encoded visual predictions and haptic evaluations of grasp  
479 comfort. To this end, once an imaging session was completed, we asked participants  
480 (while still lying in the scanner) to execute once more each of the nine grasps and  
481 rate how comfortable each felt on a scale of 1 to 10. Comfort ratings were consistent  
482 across participants (**Figure 4A**). Comfort was slightly modulated by grasp axis  
483 (**Figure 4B**,  $t(20)=3.3$ ,  $p=.0037$ ) and was not modulated by grasp size (**Figure 4C**,  
484  $t(20)=0.89$ ,  $p=.39$ ). The factor that most affected grasp comfort was object mass,

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485 with heavy objects being consistently rated as less comfortable than light objects  
486 (**Figure 4D**,  $t(20)=8.1$ ,  $p<.001$ ). This was also evident when we computed RDMs  
487 from comfort ratings (**Figure 4E**) and found that these were significantly correlated  
488 with the model RDM for object mass ( $p<.001$ ) but not with RDMs for grasp axis  
489 ( $p=.54$ ) or grasp size ( $p=.83$ ) (**Figure 4F**).

490 **Neural representations of grasp comfort were present during both grasp**  
491 **planning and execution phases.** To identify brain regions that encoded grasp  
492 comfort, we next correlated neural RDMs with the average RDM derived from  
493 participant comfort ratings. Neural representations in premotor regions PMv and  
494 PMd were significantly correlated with grasp comfort during grasp planning (**Figure**  
495 **4G**). During the execution phase instead, grasp comfort correlated with neural  
496 representations in ventral stream region PPA (**Figure 4H**). This suggests that dorsal  
497 premotor regions encoded the visually predicted comfort of planned grasps (which in  
498 our conditions was primarily related to the object mass). Area PPA instead encoded  
499 comfort during the execution phase, and might thus be involved in the haptic  
500 evaluation of grasp comfort, or some other representation of material properties that  
501 correlate with comfort.

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503 **Discussion**

504 Our results show that different regions within the two visual streams represent  
505 distinct determinants of grasping, including grasp axis, grasp size, and object mass;  
506 moreover, the coding of these attributes differed between grasp planning and  
507 execution. Most regions represented multiple factors at different stages. For  
508 example, aIPS activity correlated with both grasp axis and size during planning, and  
509 with object mass during execution. We found that grasp axis, which is adjusted at the  
510 very beginning of reach-to-grasp movements (Cuijpers et al., 2004), was  
511 predominantly encoded across dorsal regions during planning. Grasp size, which is  
512 adjusted throughout reach-to-grasp movements (Cuijpers et al., 2004), was encoded  
513 in different sets of ventral and dorsal regions during grasp planning and execution.  
514 Object mass, which gains relevance when applying forces at the fingertips upon  
515 hand-object contact (Johansson and Westling, 1988; Johansson and Flanagan,  
516 2009), was instead encoded across ventral, dorsal and motor regions during grasp  
517 execution.

518

519 **Shift from dorsal- to ventral-stream regions between planning and execution**

520 In the broadest terms, our analyses revealed an overall shift—in terms of  
521 representational similarity—from dorsal sensory and motor regions during the  
522 planning phase (**Figure 3AB**) to more ventral regions during execution (**Figure**  
523 **3CD**). During planning, the most similar representations were between V1 and  
524 SPOC, SPOC and M1/S1, and between M1/S1, PMd and aIPS, tracing an arc along  
525 the dorsal stream to frontal motor areas. SPOC is associated with representations of  
526 grasp axis (Monaco et al, 2011), as is parieto-occipital area V6A in the macaque,

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527 which together with V6 is thought to be the macaque homologue of human SPOC  
528 (Fattori et al., 2004, 2009, 2010; Pitzalis et al., 2013). The SPOC complex serves as  
529 a key node in the dorsal visual stream involved in the early stages of reach to grasp  
530 movements (Rizzolatti and Matelli, 2003). It is thus interesting to speculate that our  
531 findings likely represent the progressive transformation of grasp-relevant sensory  
532 representations of an object into explicit motor plans along the dorsal processing  
533 hierarchy. In contrast, along the ventral stream, individual ROIs (V1, LOC, PPA,  
534 pFS) shared similar representations with dorsal sensorimotor areas (particularly  
535 aIPS, M1/S1 and PMd), but only weak or no correlation with one another (or with  
536 PMv). During planning there was no visual movement to drive common responses  
537 and it seems reasonable to assume that different ROIs extracted distinct aspects of  
538 the stimulus, leading to these rather weak correlations.

539 During action execution, the picture changed dramatically. Representations in the  
540 dorsal stream became more independent from one another. Notably, the high  
541 similarity between SPOC representations and the more frontal motor regions  
542 (M1/S1, aIPS, PMd and PMv) almost disappeared, to be replaced with a stronger  
543 correlation with ventral shape-perception area LOC. At the same time,  
544 representational correlations between ventral visual regions V1, LOC, PPA and pFS,  
545 as well as their correlations with PMv increased. This may partly be due to the  
546 salient visual consequences of the participant's own actions providing a common  
547 source of variance across regions. It is interesting to speculate that the overall shift  
548 from similar dorsal to similar ventral representations reflects a shift—from the  
549 extraction of action relevant visual information during planning—to monitoring object  
550 properties to assess the need for corrections during action execution.

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551 One of the more striking findings from representational similarity analysis (**Figure**  
552 **3E,F**) is that activity in V1 during execution correlated with representations in a slew  
553 of high visual and sensorimotor areas during the planning phase (this is visible as  
554 the column of dark values below V1 in **Figure 3E**, and as the large and dense  
555 pattern of connections towards V1 in the Sankey plot in **Figure 3F**).

556 We speculate that the shift in representations between planning and execution might  
557 reflect a role of mental simulation in grasp planning and subsequent comparison to  
558 the sensory evidence during execution. During the planning phase, participants may  
559 be utilizing visual information to compute and compare forward models of potential  
560 grip choices (Wolpert and Flanagan, 2001; Cisek and Kalaska, 2010), and possibly  
561 mentally simulating potential grasps (Jeannerod, 1995; Jeannerod and Decety,  
562 1995). These simulations could be used to generate motor plans and sensory  
563 predictions. Sensory predictions could then be compared to visual, tactile, and  
564 proprioceptive inputs during the grasping phase, to facilitate online movement  
565 corrections and evaluate the success of the generated motor plan (Desmurget and  
566 Grafton, 2000; Wolpert and Ghahramani, 2000; Wolpert et al., 2011). This possibility  
567 is supported by recent work showing that planned actions can be decoded from  
568 activity in V1 and LOC before movement onset (Gallivan et al., 2013a, 2019;  
569 Gutteling et al., 2015; Monaco et al., 2020), and that V1 and LOC are re-recruited  
570 when performing delayed actions toward remembered objects (Singhal et al., 2013).

571

#### 572 **Effects of grasp comfort**

573 Grasp comfort was moderately correlated with object mass ( $r \sim 0.3$ ) but not grasp  
574 axis nor grasp size, suggesting that other factors also affected comfort (perhaps

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575 even more so than usual because of the movement constraints in the scanner).  
576 Grasp comfort was significantly correlated with PPA activation during execution,  
577 perhaps related to a role for PPA in also coding object mass during execution. More  
578 interestingly, activation patterns in premotor cortex (PMv and PMd) were correlated  
579 with grasp comfort during planning, even though no regions significantly represented  
580 object mass during planning. These results corroborate earlier results implicating  
581 premotor cortex in grip selection based on orientation (Martin et al., 2011; Wood et  
582 al., 2017) and extend the findings to a broader range of factors and to multivariate  
583 representations.

584

#### 585 **Limitations and future directions**

586 One notable finding of our study is that object mass is encoded in sensorimotor  
587 regions during action execution. This is understandable, as information about object  
588 mass is required to modulate grip and lift forces. However, we have previously  
589 demonstrated that mass and mass distribution also play an important role in  
590 selecting where to grasp an object (Klein, Maiello et al., 2020). It is thus reasonable  
591 to expect processing of object material and mass also during planning, which we did  
592 not observe. However, in our study, grasps were preselected. As a result,  
593 participants did not need to process an object's material properties to select  
594 appropriate grasp locations. In order to investigate the role of visual material  
595 representations in grasp selection, future research could use our computational  
596 framework (Klein, Maiello et al., 2020; Maiello et al., 2021) to identify objects that  
597 produce distinct grasp patterns, rather than constraining participants to predefined  
598 grasp locations. Conditions that require visual processing of object material  
599 properties to select appropriate grasp locations would then reveal whether the same

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600 or different sensorimotor regions process object mass during grasp planning and  
601 execution. However, such designs would require disentangling activity related to  
602 representing shape *per se* from activity related to grasp selection and execution.

603 One factor which is known to be important for grasp selection and execution is grip  
604 torque, i.e., the tendency of an object to rotate under gravity when grasped away  
605 from its centre of mass (Goodale et al., 1994; Lederman and Wing, 2003; Eastough  
606 and Edwards, 2006; Lukos et al., 2007; Paulun et al., 2016). While torque is directly  
607 related to object mass, it is possible to select different grasps on the same object  
608 which produce substantially different torques (Maiello et al., 2021). Since grasps with  
609 high torque require greater forces at the fingertips to maintain an object level,  
610 humans tend to avoid such high-torque grasps (Klein, Maiello et al., 2020). We  
611 originally designed our stimuli in the hope of dissociating torque from object mass.  
612 Unfortunately, in pilot testing we observed that certain object and grip configurations  
613 in the magnetic field of the MRI scanner produced eddy currents in the brass  
614 portions of our stimuli. These currents caused unexpected magnetic forces to act on  
615 the stimuli, which in turn altered fingertip forces required to grasp and manipulate the  
616 objects. To avoid the occurrence of such eddy currents in our experiment, we  
617 decided to forgo conditions differentiating the effects of object mass from those of  
618 grip torques. By employing nonconductive materials, in future work our approach  
619 could be extended to test whether grasp-relevant torque computations occur in the  
620 same visuomotor regions responsible for estimating object material and shape.  
621 While previous studies have investigated material and shape largely independently,  
622 one intriguing question for future research is how material and shape are combined  
623 to assess the distribution of materials and the consequences of mass distribution on  
624 torque and grip selection.

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628 **Conclusions**

629 Taken together, our results extend previous behavioral and modelling findings about  
630 how participants select optimal grasps based on myriad constraints (Klein, Maiello et  
631 al., 2020) to reveal the neural underpinnings of this process. Results show that  
632 distinct factors – grip orientation, grip size, and object mass – are each represented  
633 differently. Moreover, these representations change between grasp planning and  
634 execution. Representations during planning rely relatively more heavily on the dorsal  
635 visual stream, while those during execution rely relatively more heavily on the ventral  
636 visual stream. Though surprising, this transition can be explained by a transition from  
637 grip selection during planning to monitoring of sensory feedback during grasping  
638 execution.

639

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855 **Figure and Table Legends**

856 **Table 1. Regions of interest and their peak x-, y-, and z-coordinates in MNI**  
 857 **space.** Search terms used on neurosynth.org with the number of studies the meta-  
 858 analyses were based on and the extraction date (when the files were downloaded).  
 859 V1-coordinates were taken from (Wang et al., 2015).

ROIs in the left hemisphere	Centre			Search term ( <i>neurosynth</i> )	Based on # of studies	Extraction date
	X	Y	Z			
V1 (primary visual)	(Wang et al., 2015)					
LOC (lateral occipital cortex)	-42	-78	-6	<i>lateral occipital</i>	226	July 17 2020
pFS (posterior fusiform sulcus)	-36	-45	-18	<i>objects</i>	692	May 14 2020
PPA (parahippocampal place area)	-30	-45	-9	<i>place</i>	189	Feb. 18 2021
SPOC (superior parietal occipital cortex)	-18	-78	39	<i>reaching</i>	99	June 25 2019
aIPS (anterior intraparietal area)	-42	-33	45	<i>grasping</i>	90	June 25 2019
PMv (ventral premotor)	-56	7	31	<i>grasping</i>	90	June 25 2019
PMd (dorsal premotor)	-24	-12	60	<i>grasping</i>	90	June 25 2019
M1/S1 (primary sensory/motor)	-33	-27	63	<i>grasping</i>	90	June 25 2019

860

861 **Figure 1. Study design. (A)** Participants in the MRI scanner were cued to grasp 3D  
 862 objects at specific locations marked by coloured stickers. **(B)** Sequence of events for  
 863 one example trial during which participants were instructed to grasp the object at the  
 864 predefined location marked by different colour dots or arrows. Trials began by  
 865 illuminating the workspace. Through earphones, participants heard the “plan”  
 866 instruction, followed by an auditory cue (“blue”, “green”, or “red”) specifying which  
 867 grasp to execute based on the coloured stickers marking grasp locations on the  
 868 objects. This initiated the planning phase of the trial. After a jittered delay interval (6–  
 869 12 s), participants heard the “lift” command, instructing them to perform the required  
 870 grasp. This initiated the execution phase of the trial, in which participants had 7 s to

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871 execute the grasp and return their hand to the start position. Vision of the workspace  
872 was then extinguished, and participants waited for the following trial to begin. **(C)**  
873 Preselected grasps on stimulus objects of wood and brass produced nine distinct  
874 conditions designed to differentiate three components of grasping using RSA. **(D-F)**  
875 RDMs for grasp axis, grasp size, and object mass. Coloured cells represent  
876 condition pairs with zero dissimilarity, white cells represent maximum dissimilarity.  
877 **(G)** An example RDM computed from fMRI BOLD activity patterns in region PMv of  
878 one participant during the planning phase. Note the strong similarity to the grasp axis  
879 RDM in panel D. **(H)** Visualization of the selected ROIs within the Colin27 template  
880 brain. All ROIs except V1 were built as spheres centred on coordinates recovered  
881 from neurosynth.org. V1 coordinates were taken from the (Wang et al., 2015) atlas.  
882 Note that surface-rendering is for presentation purposes only as data were analysed  
883 in volumetric space and no cortex-based alignment was performed.

884

885 **Figure 2. RSA results.** **(A)** Mean neural RDMs computed in the nine ROIs included  
886 in the study. For visualization purposes only, RDMs within each region are first  
887 averaged across participants and then normalized to the full range of the LUT. **(B-G)**  
888 Correlations between model and neural RDMs in each brain ROI during planning  
889 (top, B,D,F) and execution phases (bottom, C,E,G). In bar graphs, grey shaded  
890 regions represent the noise ceiling for each ROI. Bars are means, error bars  
891 represent 95% bootstrapped confidence intervals. The same data are represented  
892 topographically as dots scaled proportionally to the mean correlation in each region.  
893 Bright colours represent significant positive correlations ( $p < .05$  with FDR correction);  
894 correlations shown in dark colours are not statistically significant.

895

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896 **Figure 3. The representational structure of grasping.** (A) Matrix showing  
897 correlations of data RDMs between regions during the planning phase. White  
898 asterisks represent significant correlations ( $p < .05$  with Bonferroni correction). (B)  
899 The same data in A are shown through hierarchical clustering and 2D  
900 multidimensional scaling, and significant correlations are shown topographically.  
901 (C,D) As in A, except for the planning phase. (E) Correlations between ROIs across  
902 planning and execution phases. (F) Sankey diagram depicting significant correlations  
903 from E.

904

905 **Figure 4. Grasp comfort.** (A) Average grasp comfort ratings for each grasp  
906 condition in the fMRI experiment. (B,C,D) Grasp comfort ratings averaged across (B)  
907 grasp axis, (C) grasp size, and (D) object mass. (E) Average RDM computed from  
908 participant comfort ratings. (F) Correlations between grasp comfort and model  
909 RDMs. (G,H) Correlations between grasp comfort and neural RDMs in each brain  
910 ROI during planning (top, G) and execution phases (bottom, H). In bar graphs, grey  
911 shaded regions represent the noise ceiling for each ROI. Bright blue bars represent  
912 significant positive correlations ( $p < .05$  with FDR correction); correlations shown in  
913 dark blue are not statistically significant. The same data are represented  
914 topographically as dots scaled proportionally to the mean correlation in each region.  
915 Across figure panels, bars are means, error bars represent 95% bootstrapped  
916 confidence intervals. \*\* $p < 0.01$ , \*\*\* $p < 0.001$

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