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The representation of observed actions at the subordinate, basic and superordinate level

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39 **Abstract**

40 Actions can be planned and recognized at different hierarchical levels, ranging from very specific
41 (e.g., to swim breaststroke) to very broad (e.g., locomotion). Understanding the corresponding
42 neural representation is an important prerequisite to reveal how our brain flexibly assigns meaning
43 to the world around us. To address this question, we conducted an event-related fMRI study in male
44 and female human participants in which we examined distinct representations of observed actions
45 at the subordinate, basic and superordinate level. Utilizing multiple regression representational
46 similarity analysis in predefined regions of interest, we found that the three different taxonomic
47 levels were best captured by patterns of activations in bilateral LOTC, showing the highest similarity
48 with the basic level model. A whole-brain multiple regression RSA revealed that information unique
49 to the basic level was captured by patterns of activation in dorsal and ventral portions of the LOTC
50 and in parietal regions. By contrast, the unique information for the subordinate level was limited to
51 bilateral occipitotemporal cortex, while no single cluster was obtained that captured unique
52 information for the superordinate level. The behaviorally established action space was best captured
53 by patterns of activation in the LOTC and superior parietal cortex, and the corresponding neural
54 patterns of activation showed the highest similarity with patterns of activation corresponding to the
55 basic level model. Together, our results suggest that occipitotemporal cortex shows a preference for
56 the basic level model, with flexible access across the subordinate and the basic level.

57

58 **Keywords:** action categorization; action observation; action recognition.

59

60 **Significance statement**

61 The human brain captures information at varying levels of abstraction. It is debated which brain
62 regions host representations across different hierarchical levels, with some studies emphasizing
63 parietal and premotor regions, while other studies highlight the role of the lateral occipitotemporal
64 cortex. To shed light on this debate, here we examined the representation of observed actions at the
65 three taxonomic levels suggested by Rosch et al. (1976). Our results highlight the role of the LOTC,
66 which hosts a shared representation across the subordinate and the basic level, with the highest
67 similarity with the basic level model. These results shed new light on the hierarchical organization of
68 observed actions and provide insights into the neural basis underlying the basic level advantage.

69

70

71 **Introduction**

72 Depending on the circumstances, different aspects of an action become relevant. As an example, we
73 might be interested in the type of punch when watching a boxing match, while we might be more
74 concerned with the broader distinction between attacking and greeting when approaching a
75 stranger at night. How the brain adapts its representational states to achieve this flexibility is a key
76 question in Cognitive Neuroscience.

77
78 The hierarchical organization of objects has been studied for decades (e.g. Gauthier et al., 1997;
79 Mack et al., 2008; Carlson et al., 2013; Iordan et al., 2015). Rosch et al., (1976) argued that objects
80 can be organized into the superordinate (e.g., furniture), basic (e.g., chair) and subordinate level
81 (e.g., kitchen chair), depending on the degree of abstraction, and that the basic level plays a central
82 role in categorization, e.g. in terms of the number and types of features used to describe an object,
83 and in terms of the speed of processing (see also Grill-Spector and Kanwisher, 2005; Mack et al.,
84 2008; Macé et al., 2009). Moreover, different taxonomic levels of objects have been shown to be
85 dissociated at the neural level (Kriegeskorte et al., 2008; Iordan et al., 2015; Dehaqani et al., 2016),
86 and it has been proposed that the ventral temporal cortex (VTC) has flexible access to these
87 different levels (Grill-Spector and Weiner, 2014).

88
89 Likewise, the planning and control of actions is assumed to be organized hierarchically (Gallivan et al.,
90 2013; Kadmon Harpaz et al., 2014; Krasovsky et al., 2014; Ariani et al., 2015; Gallivan and Culham,
91 2015; Turella et al., 2020). Similar hierarchies have been proposed to underlie the organization of
92 observed actions. Several authors distinguished between the *How*, *What* and *Why* level (e.g.
93 Vallacher and Wegner, 1985; Wegner and Vallacher, 1986; Spunt et al., 2016). Hamilton and Grafton
94 (2006, 2008) distinguished between the *goal* level (corresponding to the purpose/ outcome of an
95 action), the *muscle level* and the *kinematic level*, while Wurm and Lingnau (2015) distinguished
96 between different levels of abstraction (e.g. opening versus closing a bottle).

97
98 It is assumed that areas involved in action recognition should show invariance to the way the actions
99 are performed (e.g. Wurm and Lingnau, 2015; Hamilton and Grafton, 2006, 2008; Oosterhof et al.,
100 2010, 2012). Several studies have highlighted the role of parietal and premotor regions for action
101 representations at the *Goal* level that generalize across the *muscle or kinematic* level (Hamilton and
102 Grafton, 2006, 2008; Majdandić et al., 2009; see also Lanzilotto et al., 2020; Aflalo et al., 2020).
103 Wurm and Lingnau (2015) revealed representations of observed actions at a concrete level (specific
104 for the object and kinematics) in the LOTC, IPL and ventral premotor cortex (PMv), whereas
105 representations at an abstract level (generalizing across object and kinematics) were restricted to
106 the IPL and LOTC (see also Wurm et al., 2016). In sum, previous studies successfully distinguished
107 between observed actions at varying hierarchical levels, with some studies highlighting the role of
108 parietal and premotor regions, whereas other studies emphasize the role of the LOTC. However, to
109 the best of our knowledge, no previous neuroimaging study directly compared the three taxonomic
110 levels proposed by Rosch et al. (1976). The current study aims to fill this gap.

111
112 Zhuang and Lingnau (2021) examined the characteristics of observed actions at the three taxonomic
113 levels. Actions at the three levels differed with respect to the number and type of features
114 participants used to describe them, and in their ratings of abstraction. Moreover, participants
115 verified the action category faster at the basic and subordinate level in comparison to the
116 superordinate level. Together, these results suggest that the basic level holds the maximized
117 information, consistent with the basic level advantage reported for objects (Rosch et al., 1976).
118 Given these behavioral results, here we aimed to determine which brain regions (a) represent
119 observed actions at the three taxonomic levels, and (b) which brain regions host a joint
120 representation across these levels.

121

122 Methods**123 Overall rationale and hypotheses**

124 To reveal which brain areas represent actions at the three taxonomic levels, we separated twelve
125 daily actions into three action categories at the superordinate level (see also Zhuang and Lingnau,
126 2021). Each superordinate action category consisted of two types of actions at the basic level, and
127 each basic level action encompassed two actions at the subordinate level (Figure 1). To verify this
128 hierarchy, we used a multi-arrangement experiment (Kriegeskorte and Mur, 2012) combined with
129 inverse multidimensional scaling (MDS) and hierarchical cluster analysis. Next, to determine which
130 brain areas represent observed actions at the three different hierarchical levels, we conducted an
131 fMRI experiment and carried out ROI-based and whole-brain searchlight-based representational
132 similarity analysis (RSA; Kriegeskorte et al., 2008). Specifically, we examined the representation of
133 observed actions at the subordinate, basic and superordinate level, and the representation of the
134 behavioral similarity structure resulting from the multi-arrangement experiment.

135 We expected that the subordinate level model is represented by patterns of activations in early
136 visual areas, the LOTC and possibly the IPL and the PMv (see also Wurm and Lingnau, 2015). The
137 basic level model was expected to be represented in the LOTC and the IPL, but not in the PMv,
138 whereas the superordinate level was expected to be represented in anterior portions of the LOTC
139 (Wurm and Lingnau, 2015). The behavioral model was expected to be captured by neural patterns of
140 activation in the LOTC and possibly the IPL (Tucciarelli et al., 2019; Tarhan et al., 2021).

141 Stimulus selection and validation

142 Stimuli consisted of static images of twelve different actions (600 x 480 pixels, 14.36 x 11.07 degree
143 of visual angle; six exemplars each; see Figure 1 for an overview of stimulus exemplars and
144 corresponding action words). The twelve actions were chosen on the basis of a series of rating and
145 behavioral studies (Zhuang and Lingnau, 2021) that we briefly summarize here. First, we selected
146 action verbs corresponding to the basic level from Levin (1993). Using these action verbs, we carried
147 out a semantic similarity rating, followed by hierarchical cluster analysis. Based on the resulting
148 clusters, we selected a subset of basic level actions, excluding actions that might be hard to portray
149 as a picture (e.g. to learn, to memorize). To select labels for the superordinate level, a new set of
150 participants was provided with the basic level labels of actions belonging to a given cluster revealed
151 by the hierarchical cluster analysis. To select actions belonging to the subordinate level, participants
152 were provided with different action verbs corresponding to the basic level and were asked to
153 generate action verbs corresponding to the subordinate level. Next, another group of participants
154 was asked to rate (a) the relationship between actions at the subordinate and the superordinate
155 level (e.g. between 'swim front crawl' and 'locomotion', or between 'swim front crawl' and
156 ingestion') and (b) the degree of abstraction and complexity of each action at the subordinate level.
157 Actions were only included in the final set if they were consistently rated to belong to a given
158 superordinate category, and not to other superordinate categories.

159 We selected the six different exemplars for each of the twelve actions based on the following criteria:
160 young adult agents of both genders, with an equal representation of three males and three females
161 per action. In addition, we selected three distinct orientations for each agent, including two profile
162 views (facing left and right, respectively) and one frontal view. Note that for the action 'doing the
163 dishes', we replaced frontal views by another profile view exemplar due to the lack of suitable
164 images depicting this action in a frontal view.

165 Since the rating studies were based on written words, we first wanted to verify how human
166 participants categorize these actions when presented as static images. To this aim, we carried out a
167 multi-arrangement experiment (Kriegeskorte et al., 2008) as implemented in the online platform
168 MEADOWS (<https://meadows-research.com>) in a group of N=18 participants (12 female; mean age:
169 27 years; range: 22-31 years) that did not take part in the fMRI experiment. Participants were
170 instructed to judge the degree of similarity between the twelve actions depicted in these static

171 images, to arrange them accordingly (i.e., the more similar in meaning, the closer they should be
172 positioned on the screen), and to press a button when they were satisfied with the arrangement of
173 the stimuli. In the first trial, all stimuli appeared on the screen (stimulus size: 48 x 38 pixel). In all
174 subsequent trials, an adaptive algorithm chose a subset of all stimuli in order to provide the optimal
175 evidence for pairwise dissimilarity estimates (see Kriegeskorte and Mur, 2012, for details). The
176 experiment continued until the adaptive algorithm reached the required evidence level for pairwise
177 dissimilarities. The full stimulus set contained 72 static images (12 actions x 6 exemplars). Each
178 participant was provided with 12 different actions. Action exemplars were counterbalanced across
179 participants.

180
181 Results of the multi-arrangement experiment were collapsed across participants and averaged
182 across image exemplars. We visualized the results by creating a 12 x 12 representational dissimilarity
183 matrix (RDM) where each cell contains a value corresponding to the Euclidean distance between two
184 actions (Figure 2A). Figure 2B shows a 2-dimensional (2D) arrangement MDS derived from
185 multidimensional scaling (metric stress), averaged across participants. Inverse MDS revealed three
186 larger clusters corresponding to the three superordinate action categories. Subsequently, to reveal
187 the corresponding hierarchical structure, we carried out average-linkage hierarchical cluster analysis
188 (using the Matlab function *linkage*) on the results obtained from the multi-arrangement experiment.
189 The results are shown in Figure 2C. This analysis confirmed the hierarchical structure of the selected
190 actions, with three action categories corresponding to the superordinate level (locomotion,
191 ingestion and cleaning), six action categories at the basic level (to swim, to ride, to eat, to drink, to
192 clean the body and to do housework), and twelve actions at the subordinate level (to ride a
193 motorbike, to ride a bike, to swim front crawl, to swim backstroke, to drink water, to drink beer, to
194 eat cake, to eat an apple, to clean windows, to do the dishes, to brush teeth, and to clean the face).

195

<< Figure 1 >>

196

197

<< Figure 2 >>

198

199

200

Participants

201 A group of N=23 participants (17 female; mean age: 26 years; range: 21- 39 years) took part in the
202 fMRI experiment. All participants except two authors of the paper (T.Z. and Z.K.) were naive to the
203 purpose of the study. All participants gave written informed consent before joining the experiment
204 and received either monetary compensation or course credits at the University of Regensburg. All
205 participants had normal or corrected-to-normal vision and reported to have no psychiatric or
206 neurological disorders.

207

208

fMRI experimental design and task

209 We used a rapid event-related fMRI design (see Figure 3), programmed in ASF (Schwarzbach, 2011),
210 adopting the design used by Tucciarelli et al., (2019). During each trial, participants were provided
211 with a static image of an action and a central fixation cross superimposed on the image (1 s),
212 followed by a blank screen and a central fixation cross (3 s). Participants were instructed to observe
213 the action while keeping their eyes at fixation. During occasional catch trials (11% of all trials),
214 participants were presented with a phrase depicting an action (e.g. 'to swim?', 1 s) followed by 3 s
215 fixation. During catch trials, participants had to perform a category verification task. Specifically,
216 they were instructed to indicate by button press with the index or middle finger of the right hand
217 whether or not the action shown in the previous trial corresponded to the phrase shown during the
218 catch trial. To make sure that participants were not biased towards answering questions at one of
219 the three different levels, phrases presented during catch trials had an equal probability to address
220 the superordinate (e.g. 'locomotion?'), basic (e.g. 'to swim?') or subordinate ('to swim
221 breaststroke?') level. That is, there was the same number of catch trials for each of the three

222 taxonomic levels (four catch trials per taxonomic level in each run). Additionally, to improve design
223 efficiency, we included null events (22.2% of all trials) that consisted of 4 s fixation and were
224 presented pseudo-randomly (no consecutive null events and catch trials).

225

226

<< Figure 3 >>

227

228 Participants performed six runs, each consisting of 72 experimental trials (66.7%), 12 catch trials
229 (11.1%) and 24 null events (22.2%). Additionally, each run included a 10 s fixation period at the
230 beginning and the end. Each run lasted 7.5 minutes. Halfway throughout the experiment, an
231 anatomical scan was performed with a duration of approximately 5 minutes. The whole experiment
232 lasted approximately 50 minutes. To ensure that participants fully understood and followed the
233 instructions, participants performed a short practice run (consisting of 12 trials) prior to entering the
234 scanner.

235

236 **Data acquisition**

237 The experiment was conducted in the MRI laboratory at the University of Regensburg. Data were
238 collected using a 3T full-body Siemens-Prisma scanner with a 64-channel head coil. A T2*-weighted
239 gradient multiband (MB) echo-planar imaging (EPI) sequence was used for acquiring functional
240 images with 64 slices per volume, using the following parameters: repetition time (TR): 2s, Echo
241 Time (TE): 30 ms, flip angle: 75°, excitation pulse duration = 9 ms; echo spacing = 0.58 ms; bandwidth
242 = 2368 Hz/ pixel; Field of view (FoV): 192*192 mm², partial Fourier = 6/8; voxel resolution: 2.5 mm³,
243 MB-acceleration: 4. Each functional run consisted of 226 volumes and lasted 7 min and 32 s.
244 Between the third and fourth EPI sequence, we acquired a 5 min T1-weighted Magnetization
245 Prepared Rapid Gradient Echo (MPRAGE) structural sequence (TR: 1910 ms, TE: 3.67 ms, FOV:
246 256*256 mm, voxel size: 1 mm³, flip angle: 9°).

247

248 **fMRI data preprocessing**

249 We used the FMRIB Software Library (FSL 6.0 <https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>) to preprocess the
250 data. The first four volumes were deleted from each functional run to ensure to have reached
251 steady-state magnetization. Functional images were slice time corrected, highpass filtered (with a
252 cut-off of 100 s), corrected for head-motion with 7 degrees of freedom (DOF) and the middle volume
253 as reference, and then co-registered to the individual T1 anatomical image. For univariate analysis,
254 functional data were smoothed with a 5-mm full width half maximum (FWHM) kernel. For
255 multivariate analysis, we used unsmoothed data. Data were aligned into Montreal Neurological
256 Institute (MNI) space.

257

258 **Region of interest (ROI) definition**

259 ROI definition was carried out using a combination of functional data and anatomical masks
260 obtained from the Harvard-Oxford Cortical structural and the Jülich Histological atlas (see Table 1).
261 We focused on key areas of the action observation network described in previous studies (e.g., Grill-
262 Spector and Kanwisher, 2005; Hamilton and Grafton, 2008; Grafton and Hamilton, 2009; Kilner, 2011;
263 Binkofski and Buxbaum, 2013; Héту et al., 2013; Hoffman et al., 2015; Wurm et al., 2017b).
264 Specifically, we selected the bilateral LOTC, IPL, SPL, dorsal premotor cortex (dPM), and IFG. In
265 addition, to be able to compare results with an area concerned with low-level visual analysis, we
266 identified bilateral V1.

267

268 ROI definition consisted of several steps. First, we computed the random-effects (RFX) general linear
269 model (GLM) contrast 'all actions versus baseline' with spatially smoothed data (5mm FWHM). The
270 baseline consisted of all events not explicitly modelled in the GLM. The RFX GLM included seventy-
271 two regressors (12 actions x 6 exemplars), one regressor for the catch trials, and six regressors for
272 head motion. The statistical map resulting from the RFX GLM contrast was corrected for multiple

273 comparisons using Threshold-Free Cluster Enhancement (TFCE, Smith and Nichols, 2009, $p < 0.05$,
274 $|z| > 1.96$, two tailed, 5000 permutations) as implemented in CoSMoMVPA (Oosterhof et al., 2016;
275 <http://cosmomvpa.org/index.html>). Second, we defined anatomical masks from the Harvard-Oxford
276 Cortical structural and the Jülich Histological atlas (threshold: 20%; see Table 1 for details). The mask
277 for the LOTC was created by merging the anatomical masks for the inferior lateral occipitotemporal
278 cortex (LOC) and the occipito-temporal cortex. Third, within each resulting mask, we extracted the
279 peak coordinate resulting from the RFX GLM contrast 'all actions vs baseline'. ROIs were defined as
280 spheres (radius: 10 mm) centered around these peaks.

281
282
283

<< Table 1 >>

284 **Representational similarity analysis**

285 We carried out RSA using the CoSMoMVPA Toolbox (Oosterhof et al., 2016) and custom written
286 Matlab functions (available at <https://osf.io/b6ea4/>). We used the following procedure both for the
287 ROI-based and the whole-brain searchlight approach unless otherwise noted.

288

289 **ROI-based RSA (partial correlations)**

290 To examine the representation of observed actions in predefined ROIs, we used RSA with partial
291 correlations (Kriegeskorte et al., 2008). First, we created a model RDM for each of the three
292 taxonomic levels (Figure 1, bottom panel), corresponding to the hierarchical structure shown in
293 Figure 1 (top panel; see also Zhuang and Lingnau, 2021). Since we used 6 exemplars for each of the
294 12 actions, each model RDM consisted of a 72×72 matrix, where each cell in the matrix corresponds
295 to the dissimilarity between a pair of actions. The subordinate level model consists of twelve clusters
296 along the diagonal, with each cluster comprising six exemplars of the same type of action. The basic
297 level model consists of six clusters along the diagonal, while the superordinate model consists of
298 three clusters along the diagonal.

299

300 Second, to account for differences between the different action categories in terms of low-level
301 visual properties, we constructed a control model using the 1st layer of a Deep Neural Network (DNN)
302 that has been trained to classify image classes in the ImageNet dataset (ResNet50, He et al., 2015).
303 We chose this layer because the first layer of a deep neural network is generally assumed to learn to
304 detect edges, colours, texture orientations and other simple shapes in input images (Zeiler and
305 Fergus, 2014; Kriegeskorte, 2015; Mahendran and Vedaldi, 2015). For each of the 72 images used in
306 the current experiment, we determined the activations of each unit in the first convolutional layer of
307 the ResNet50 and converted these values into activation vectors, separately for each image. Next,
308 we constructed the 72×72 low-level visual control model by computing the dissimilarity (1-
309 correlation) between these activation vectors for each pair of action images (for similar approaches,
310 see Kriegeskorte et al. 2008, 2012). Additionally, to account for features related to the scene or
311 background in which the action took place, we created a 72×72 scene control model. We used the
312 same procedure as the one described for the construction of the low-level visual control model. The
313 only difference was that we obtained activations in response to each image from the second-to-last
314 layer of the ResNet50 trained on a large image dataset to distinguish between scene categories
315 (Zhou et al., 2017, 2018).

316

317 Third, we constructed neural RDMs within each ROI following previous studies (Bonner and Epstein,
318 2018; Tucciarelli et al., 2019). To do so, separately for each run and each of the 72 action images (12
319 actions \times 6 exemplars), we extracted the beta estimates for each voxel in a given ROI and converted
320 these beta estimates into t-values, resulting in a vector of t-values for each action image, with the
321 length corresponding to the number of voxels. Next, we averaged the t-values across runs and
322 normalized the t-values by subtracting the mean t-values of each voxel from the t-values of each
323 action image (Diedrichsen and Kriegeskorte, 2017), separately for each participant. Finally, for each

324 of the 72 x 72 pairwise comparisons of action images, we computed the squared Euclidean distance
325 between the corresponding vectors of t-values, resulting in a 72 x 72 neural RDM.

326

327 Finally, to determine which of the ROIs captured the similarity between actions at the three
328 taxonomic levels, we computed partial correlations between neural RDMs and each of the three
329 model RDMs, regressing out the low-level visual control model and the scene control model.

330

331 **Searchlight-based RSA (multiple regression)**

332 To determine whether additional areas not captured by the ROI analysis contained information
333 regarding observed actions at the three taxonomic levels, we carried out two different multiple-
334 regression representational similarity analyses (RSAs). In both types of searchlight-based RSAs, we
335 used a spherical neighborhood of 100 voxels which were nearest to each center voxel. As in the ROI
336 analysis, t values were averaged across runs and normalized by subtracting the mean t-value of each
337 voxel across conditions.

338

339 To examine risks of multicollinearity, we determined the Variance Inflation Factor (VIF) for the three
340 taxonomic models depicted in Figure 1 (bottom panel), the low-level visual control model and the
341 scene control model. We obtained small to moderate VIFs (subordinate model: 1.90; basic model:
342 2.55; superordinate model: 1.78; low-level visual control model: 1.31, scene control model: 1.77),
343 suggesting a low risk of multicollinearity (Mason et al., 2003).

344

345 In the first multiple regression RSA, computed separately for each taxonomic level, we included the
346 model for a single taxonomic level (e.g. the subordinate level), the low-level visual control model
347 and the scene control model. This allowed us to obtain beta weights for each taxonomic level while
348 regressing out the low-level visual control model and the scene control model.

349

350 In the second multiple regression RSA, we aimed to determine the unique contribution of each
351 taxonomic level. To this aim, we set up a multiple regression that included all three taxonomic level
352 models, the low-level visual control model and the scene control model. This way, we were able to
353 obtain the beta weights for each of the three taxonomic levels while regressing out the contribution
354 of the other two taxonomic levels, the low-level visual control model and the scene control model.

355

356 Finally, in order to examine the relationship between neural RDMs and the behavioral dissimilarity
357 matrix obtained from the multi-arrangement task (see Figure 2B), we carried out another
358 searchlight-based multiple regression RSA in which we included (a) the behavioral model, the low-
359 level visual control model and the scene control model, and (b) the behavioral model, each of the
360 taxonomic models separately, the low-level visual control model and the scene control model. VIFs
361 were also computed and the results were small to moderate, justifying the use of multiple
362 regression RSA. In particular, the VIFs for the low-level visual control model, the scene control model
363 and the behavioral model were small (low-level visual control model, scene control model and
364 behavioral action space model: VIF=1.31, 1.85, 1.53, respectively). Additionally, the VIFs for
365 regression models including the behavioral action space model, each of the taxonomic level models,
366 the low visual control model and the scene control model were small to moderate (behavioral action
367 space model, subordinate level model, low-level visual control model and scene control model: VIF=
368 3.84, 3.18, 1.33, 1.88, respectively; behavioral action space model, basic level model, low-level visual
369 control model and scene control model: VIF=6.10, 5.34, 1.32, 1.88, respectively; behavioral action
370 space model, superordinate level model, low-level visual control model and scene control model:
371 VIF=2.63, 2.24, 1.31, 1.87, respectively).

372

373

374

375 **Conjunction analysis**

376 To reveal which brain regions host converging representations across the different taxonomic levels,
377 we conducted a conjunction analysis (Nichols et al., 2005). To this aim, we determined the minimum
378 t-value for each voxel for the whole-brain searchlight maps corresponding to the unique
379 representation of the different taxonomic levels (corresponding to the results shown in Figure 6B).

380

381 **Statistics**

382 For the ROI-based partial correlation analysis, we first used one-sample t-tests to compare the
383 Fisher-transformed partial correlation values against zero. Second, to determine whether the
384 similarity between neural and model RDMs depicted in Figure 4 was modulated by the taxonomic
385 level and ROI, we carried out a two-way repeated measures ANOVA with the factors *taxonomic level*
386 (superordinate, basic, subordinate) and *ROI* (see Table 1), followed by pairwise comparisons.
387 Corrections for multiple comparisons for all factorial combinations (taxonomic level x ROI) was
388 carried out using the false discovery rate (FDR; Benjamini and Hochberg, 1995). Since the
389 assumption of sphericity was violated for the 2-way ANOVA, we report Greenhouse-Geisser-
390 corrected p values (indicated as p_{GG}).

391

392 For the searchlight-based multiple regression RSA, the beta maps determined separately for each
393 participant were entered into a group statistic by means of a one-sample t-test (one-tailed) against
394 zero. The resulting t maps were corrected for multiple comparisons using threshold free cluster
395 enhancement (TFCE) as implemented in CoSMoMVPA (Oosterhof et al., 2016; number of
396 permutations=5000, corrected $p < 0.05$, $z > 1.65$, one tailed). Thresholded statistical maps were
397 visualized using BrainNet (<https://www.nitrc.org/projects/bnv/>).

398

399 **Results**

400 **Behavioral results**

401 Participants reached a high accuracy (91.1%, standard deviation: 6%) in the category verification task,
402 indicating that they paid attention to the actions depicted in the images.

403

404 **ROI-based results**

405 Figure 4 shows the results from ROI-based RSA for the three taxonomic levels, regressing out low-
406 level visual properties by means of a control model obtained from the first convolutional layer of a
407 Deep Neural Network (ResNet50_conv1; see section ROI-based RSA for details) and the scene
408 control model (based on the last second layer of ResNet50 pretrained with places; see section ROI-
409 based RSA for details). We obtained significant partial correlations between neural RDMs and all
410 three taxonomic level models in most of the examined ROIs, with the exception of the right IFG,
411 where no significant partial correlation was observed between neural RDMs and the subordinate
412 level. Similarities (partial correlation values) between neural RDMs and model RDMs differed
413 between the three taxonomic levels in bilateral LOTC and SPL. In bilateral LOTC, we obtained the
414 highest partial correlations for actions at the basic level in comparison to the other two taxonomic
415 levels. In bilateral SPL, we observed higher partial correlations between the neural RDM and the
416 basic level model in comparison to the superordinate level model.

417

418 These observations are supported by the corresponding statistics. In particular, a two-way
419 (taxonomic level x ROI) repeated measures ANOVA revealed a significant main effect of taxonomic
420 level ($F_{(2,44)} = 8.88$, $p_{GG} = .002$, partial $\eta^2 = .29$) and ROI ($F_{(11,242)} = 32.93$, $p_{GG} < .001$, partial $\eta^2 = .60$),
421 and a significant interaction between taxonomic level and ROI ($F_{(22,484)} = 3.46$, $p_{GG} < .001$, partial η^2
422 = .14). Pairwise comparisons within each ROI (using FDR to correct for multiple comparisons)
423 revealed that neural RDMs in the bilateral LOTC showed the highest similarity with the basic level
424 model in comparison to the other two models (left: basic vs subordinate level, $t_{(1,22)} = 6.11$, q_{FDR}
425 $< .001$; basic vs superordinate level, $t_{(1,22)} = 3.57$, $q_{FDR} = .003$; right: basic vs subordinate level, $t_{(1,22)} =$

426 5.04, $q_{FDR} < .001$; basic vs superordinate level, $t_{(1,22)} = 4.04$, $q_{FDR} < .001$). Additionally, neural RDMs in
427 bilateral SPL showed a higher partial correlation with the basic level model in comparison to the
428 superordinate level (left: basic vs superordinate level, $t_{(1,22)} = 3.53$, $q_{FDR} = .006$; right: basic vs
429 superordinate level, $t_{(1,22)} = 3.86$, $q_{FDR} = .003$).

430
431
432

<< Figure 4 >>

433 To illustrate the results obtained in bilateral LOTC in comparison to bilateral early visual cortex (V1),
434 Figure 5 visualizes neural RDMs (left panel) and the corresponding 2D-arrangements obtained from
435 multidimensional scaling analysis (right panel) in bilateral LOTC (top row) and bilateral V1 (bottom
436 row). Using the same approach described for the searchlight-based RSA, we created a 72 X 72 neural
437 RDM in LOTC and V1, and then collapsed the neural RDM across hemispheres and participants. Next,
438 to account for low-level visual features and scene-related properties, we extracted values from the
439 lower triangular part of the neural RDM and regressed out the corresponding lower triangular part
440 of the low-level visual control model and the scene control model. Finally, the resulting residuals
441 were rescaled to values from 0 to 100 (Nili et al., 2014). In the 2D visualization of the MDS (Figure 5B,
442 D), the three superordinate action categories are highlighted in different colors (blue, red, and
443 green), the basic action categories within a superordinate category are shown by open and filled
444 symbols, and different symbols (circles, squares) indicate the different actions at the subordinate
445 level within each basic level category. As can be seen from Figure 5, the neural RDM in bilateral LOTC
446 (Figure 5A) and the corresponding 2-D arrangement resulting from multidimensional scaling (Figure
447 5B) reveals a broad distinction into actions at the basic level, with open symbols mostly on the right
448 side and filled symbols mostly on the left side, and an additional broad clustering into the three
449 different superordinate categories highlighted in red, green and blue (Figure 5B). By contrast, this
450 pattern is less obvious in early visual cortex (Figure 5C, D), in line with the results of the ROI-based
451 analysis shown in Figure 4.

452
453
454

<< Figure 5 >>

455 Whole-brain searchlight results

456 Figure 6A reveals areas that capture the similarity between actions at the three different taxonomic
457 levels when low-level visual features and scene-related properties are regressed out via a low-level
458 visual control model and a scene control model (see Section *ROI-based RSA* for details). This analysis
459 reveals a wide set of regions for the subordinate and basic level, with peaks in the right fusiform
460 cortex (Table 2). By contrast, the representation of observed actions at the superordinate level is
461 restricted to a more circumscribed region in occipitotemporal cortex extending into the anterior IPL,
462 with a peak in right occipital pole (Table 2).

463
464

464 Figure 6B shows which areas capture the similarity structure of observed actions that is unique to
465 each of the taxonomic levels (accounting for the other two taxonomic models as well as for the low-
466 level visual features and the scene control model). This analysis reveals that the dissimilarity
467 structure for actions that is unique to the subordinate level is restricted to bilateral occipito-
468 temporal cortex, with a peak in right fusiform cortex, while information that is unique to the basic
469 level is associated with bilateral occipito-temporal cortex, IPL and SPL, with a peak in the right
470 occipital fusiform cortex (see Table 2). By contrast, we obtained no region that represented
471 information that is unique to the superordinate level. We will return to this observation in the
472 discussion.

473
474
475

<< Figure 6 >>

<< Table 2 >>

476
477

478 To identify regions in which actions are jointly represented at the subordinate and basic level, we
479 computed a conjunction analysis on the basis of the statistical maps corresponding to the unique
480 representation of the subordinate and basic level shown in Figure 6B (see Methods section for
481 details). The results are shown in Figure 7. The convergence of observed actions at the subordinate
482 and basic level was located in bilateral OTC.

483 << Figure 7 >>
484

485 **Relationship between neural RDMs and behavioral dissimilarity structure**

486 Whereas the previous analyses focused on the representation of the three taxonomic levels, we next
487 aimed to determine which brain areas capture the dissimilarity structure between observed actions
488 resulting from the multi-arrangement task, and to which degree these representations are
489 accounted for by the model RDMs corresponding to the three taxonomic levels. To address these
490 questions, we carried out two additional multiple regression searchlight analyses.

491
492 First, we ran a multiple-regression RSA between neural RDMs and the behavioral dissimilarity
493 structure shown in Figure 2A, regressing out the low-level visual control model and the scene control
494 model. As shown in Figure 8A, this analysis revealed large clusters in bilateral occipitotemporal
495 cortex, IPL, and SPL that were associated with the behavioral action space model.

496
497 Second, separately for each of the taxonomic levels, we carried out another multiple-regression RSA
498 in which we included the behavioral action space model, the low-level visual control model, the
499 scene control model and the respective taxonomic level (e.g., the subordinate level). A map of the
500 beta weights corresponding to the behavioral action space model, after regressing out the low-level
501 visual control model, the scene control model and each of the taxonomic level models are shown in
502 Figure 8B-D. As can be seen, after regressing out the subordinate level, the low-level visual control
503 model and scene control model, the behavioral action space model is associated with neural
504 patterns in bilateral occipitotemporal cortex (Figure 8B). After regressing out the superordinate
505 model (Figure 8D), the low-level visual control model and the scene control model, large regions of
506 bilateral occipitotemporal cortex, IPL and SPL remained significantly associated with the behavioral
507 action space model. By contrast, after regressing out the basic level model, the low-level visual
508 control model and the scene control model, a small cluster in the temporal occipital fusiform cortex
509 (bilaterally) and left superior LOC remained that captured the behavioral action space model (Figure
510 8C). Whereas these latter results need to be interpreted with caution, they are in line with the view
511 that the cortical representations of the behavioral action space model best reflects information at
512 the basic level (see also Figure 4 and 5). We will return to this observation in the discussion.

513 << Figure 8 >>
514

515 **Control analysis: Whole-brain searchlight analysis for the low-level visual control model**

516 To examine which brain regions show a significant correlation between neural activation patterns
517 and the control model capturing low-level visual features, we carried out an additional whole-brain
518 searchlight RSA with the low-level visual control model (*ResNet50_conv1*). The results are shown in
519 Figure 8-1. As expected, this analysis revealed clusters in early visual cortex (V1 and V2) bilaterally
520 and additionally in a small portion of the superior LOC, temporal occipital fusiform cortex and
521 inferior LOC (right hemisphere). In other words, this analysis suggests that whereas some of the
522 regions capturing low-level visual features overlap with the regions capturing the three taxonomic
523 levels and the behavioral action space model, the majority of voxels revealed by the taxonomic level
524 models and the behavioral action space model do not overlap with the regions capturing low-level
525 visual features.

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530 Discussion

531 In the current study we aimed to examine the neural representation of observed actions at different
532 taxonomic levels. Utilizing a hierarchical stimulus set and representational similarity analysis, we
533 observed the highest similarity between neural patterns and the basic level model in bilateral LOTC.
534 A searchlight RSA revealed that the similarity between observed actions at the subordinate and the
535 basic level was captured in a widespread set of occipitotemporal, parietal and frontal areas, whereas
536 neural patterns corresponding to the superordinate level model were obtained in a more
537 circumscribed region in bilateral occipitotemporal cortex. Unique information corresponding to the
538 basic level was captured by patterns of activation in lateral and ventral occipitotemporal cortex and
539 bilateral SPL, while unique information corresponding to the subordinate level was restricted to
540 bilateral occipitotemporal cortex. For the superordinate model we did not obtain any cluster that
541 captured unique information. Additionally, we found that bilateral occipitotemporal cortex jointly
542 hosted representations that are unique to the subordinate and the basic level. Finally, the behavioral
543 action space model was captured by patterns of activation in occipitotemporal and SPL, and these
544 neural patterns showed high similarity with the basic level model. Together, our results are in line
545 with the view that lateral and ventral portions of the occipitotemporal cortex have flexible access to
546 the representational space of observed actions at the subordinate and basic level, with a special role
547 for the basic level (see also Rosch et al., 1976; Zhuang and Lingnau, 2021). In the following, we will
548 discuss these points as well as limitations and directions for future studies in more detail.

549

550 The representational space of observed actions in the LOTC

551 The LOTC has been shown to distinguish between different observed actions at the basic level on the
552 basis of patterns of activation, with a generalization across the subordinate level (Wurm et al., 2016;
553 Hafri et al., 2017; Wurm and Lingnau, 2015). We previously reasoned that if the LOTC is involved in
554 processing observed actions at a conceptual-semantic level, it should not only distinguish between
555 two actions A and B, but also capture the similarity structure of a wider range of actions. Several
556 previous studies have demonstrated that this is indeed the case (Tucciarelli et al., 2019; Tarhan et al.,
557 2021), and Wurm and Caramazza (2019) furthermore showed that representations in the LOTC
558 generalize across visual stimuli and verbal descriptions of the same actions. In line with this view,
559 several authors proposed a posterior-to-anterior concrete-to-abstract gradient in the LOTC (Lingnau
560 and Downing, 2015; Wurm et al., 2017b; Papeo et al., 2019; Wurm and Caramazza, 2021).

561

562 The results of the current study extend these findings, demonstrating that the LOTC captures (a) the
563 behavioral similarity structure of a different set of actions and (b) the unique representation at the
564 subordinate and basic level, with a preference for the basic level (see also Jordan et al., 2015). Our
565 results demonstrate that the LOTC plays a crucial role in representing actions at multiple levels in a
566 situation in which participants are not biased towards processing one of these levels. An important
567 next step for future studies will be to examine the impact of the observer's goal, emphasizing one
568 level over one other. For instance, our goals (such as acquiring a new skill versus predicting the
569 intention of another agent) may determine our focus on either concrete representations at the
570 subordinate level or more abstract representations at the basic or superordinate level. Moreover,
571 these results are consistent with the view that the lateral and ventral portion of the OTC hosts and
572 integrates different action components (such as visual motion, body part, manipulation of tools, e.g.
573 Lingnau and Downing, 2015; Tucciarelli et al., 2019) at varying levels of abstraction (see also Wurm
574 and Lingnau, 2015; Wurm and Caramazza, 2021).

575

576 The importance of the basic level for the representation of observed actions

577 Previous behavioral studies suggested that the basic level holds the maximized information for
578 objects (Rosch et al., 1976; Murphy, 2004) and actions (Zhuang and Lingnau, 2021). The results of
579 the current study provide insights into the neural basis underlying these behavioral findings. First,
580 we found that patterns of activation in bilateral LOTC and SPL showed a higher similarity with the

581 basic level model in comparison to the subordinate and the superordinate level (Figure 4). Second,
582 information that is unique to the basic level was captured in more widespread regions, including
583 OTC, IPL and SPL (Figure 6B), in comparison to information that is unique to the subordinate level
584 (Figure 6A), while we did not obtain any area that captured information that is unique to the
585 superordinate level. Third, the behavioral action space model showed the highest similarity with
586 neural patterns capturing the basic level model (see Figure 8C). Together, the results of the current
587 study on observed actions are consistent with results by Jordan et al. (2015) demonstrating that
588 objects at the basic level show the strongest similarity with patterns of activation in the lateral
589 occipital cortex (LOC).

590

591 **The representation of actions at the superordinate level**

592 In contrast to the subordinate and basic level, we obtained no region that represented information
593 that is unique to the superordinate level. Given that this result is based on the absence of evidence,
594 this finding needs to be interpreted with care. There are several reasons that might account for this
595 observation: (1) lack of power; (2) there is no region that host the unique information at the
596 superordinate level; (3) information at the superordinate level is based on the combination of
597 information at the subordinate and basic level; (4) the representation of actions at the
598 superordinate level is more distributed than the representation of actions at the subordinate and
599 basic level, making it unlikely to be revealed by methods that rely on local patterns of activation
600 (searchlight, ROI analysis). In line with the latter interpretation, Abdollahi, Jastorff, and Orban (2013)
601 found that different classes of observed actions (e.g., manipulation, locomotion and climbing,
602 corresponding to the superordinate level) recruit different parts of parietal cortex. This observation
603 might explain why we failed to obtain evidence for a unique – local - representation capturing the
604 similarity between the different actions at the superordinate level. Further studies will be required
605 to distinguish between these alternatives more systematically.

606

607 **The contribution of high-level visual features and semantic knowledge to the categorization of** 608 **actions**

609 Since we did not compare the processing of visually presented actions with the processing of the
610 corresponding action verbs or phrases, we cannot clearly separate between the contribution of
611 higher-level visual features (or perceptual action precursors, see Wurm and Caramazza, 2021) and
612 semantics. As pointed out above, a study that focused on this direct comparison revealed shared
613 representations between patterns of activations for different actions depicted as videos and as
614 written sentences found this to be the case exclusively in the lateral posterior temporal cortex
615 (Wurm and Caramazza, 2019). That said, to be able to tolerate varying degrees of variability, we
616 assume that the categorization of visually presented actions requires access to semantic knowledge
617 for all three taxonomic levels, while the amount of variability is likely to differ between the levels.
618 Specifically, members of the same subordinate level are assumed to have a higher number of shared
619 features that can be exploited to categorize actions at the subordinate level (e.g. the body posture
620 to distinguish between front crawl and backstroke; see also Zhuang and Lingnau, 2021). At the basic
621 level, which is considered to be the most informative level (see e.g. Rosch et al., 1976),
622 categorization has been proposed to rely on more common features that are shared across
623 members of a category (e.g. applying some liquid to the body with hands or a tool to categorize an
624 image to belong to the basic level category ‘cleaning the body’). Finally, to distinguish actions at the
625 superordinate level, an even higher degree of generalization across high-level visual features is
626 required (e.g. bringing an object to the mouth for the category ingestion).

627

628 **Comparison of object and action representations**

629 There exists a long tradition both in human (see e.g. Bach et al., 2014, Wurm et al., 2017b; Livi et al.,
630 2019; Wurm and Caramazza, 2021) and monkey studies (e.g. Bonini et al., 2014) demonstrating that
631 objects provide strong clues regarding the actions they afford, and that objects play an important

632 role during action observation. Consequently, the representation of objects and actions have been
633 proposed to follow similar, though not identical, principles of organization (see e.g. Pillon and
634 d'Honinchtun, 2011; Wurm et al., 2017b). As an example, Wurm, Caramazza, and Lingnau (2017)
635 demonstrated that features corresponding to actions directed towards persons and objects are
636 preferentially represented in dorsal and ventral portions of the LOTC, parallel to the organization of
637 information related to persons versus inanimate objects, respectively. Given these assumed similar
638 principles of organizations, it is notoriously difficult to dissociate the representation of actions and
639 objects. That said, Tucciarelli et al. (2019) showed that patterns of activation in the LOTC capture the
640 behavioral similarity structure of actions, over and above variability due to action components such
641 as objects involved in the action. Likewise, several previous studies demonstrated representations of
642 observed actions in the LOTC that generalized across the object (Wurm and Lingnau, 2015; Wurm et
643 al., 2016). More specifically, Wurm et al. (2016) demonstrated that it is possible to distinguish
644 between observed opening and closing actions, irrespective of the object, in the LOTC, IPL and PMv,
645 whereas decoding between objects across actions was restricted to clusters in the ventral stream
646 (Wurm et al., 2016, Figures 3, 4 and Supplementary Figure 5). While we cannot clearly dissociate
647 between the representation of action functions and object states/ object affordances in the current
648 study, these previous studies indicate that action representations in the LOTC can be dissociated
649 from representations of objects that are being manipulated.

650

651 **The impact of scene-related information**

652 Like objects, due to frequent co-occurrences, scenes can provide important cues regarding the kind
653 of actions that are likely to be experienced (e.g. food-related actions in a kitchen scene and sport-
654 related actions in a gym; see also (Wurm and Schubotz, 2012, 2017; Wurm et al., 2017a). To be able
655 to account for the potential contribution of scene-related information in the current study, we used
656 the activations of the second-to-last layer of a convolutional neural network (ResNet50) trained to
657 distinguish between scene categories. A promising future step will be to systematically investigate
658 the impact of the relationship between scene and action information on the representational space
659 of actions.

660

661 **Limitations and future directions**

662 Previous studies revealed that posterior portions of the LOTC are recruited both by static images
663 (Hafri et al., 2017; Tucciarelli et al., 2019) and by dynamic videos depicting actions (Hafri et al., 2017;
664 Wurm et al., 2017b; Wurm and Lingnau, 2015). In addition, Hafri et al. (2017) successfully decoded
665 observed actions across static and dynamic input in a number of regions, including the LOTC. That
666 said, we cannot rule out that additional aspects relevant to the processing of the depicted actions, in
667 particular, the corresponding kinematics, are not well captured in the current study.

668 Moreover, while we accounted for the impact of low-level visual and scene-related features, another
669 important limitation of the current study is related to the fact that with the current stimulus material
670 we cannot discount the impact of variance shared with object-related features involved in the
671 actions. Moreover, it will be important to demonstrate to which degree the behavioral action space
672 examined in the current study generalizes to a wider range of actions. Further studies are required
673 to address these points.

674

675 **Conclusion**

676 Our results offer a neural perspective on categorical distinctions of observed actions across
677 taxonomic levels, yielding insights into the mechanisms underlying behavioral flexibility aligned with
678 the observer's goals. Lateral and ventral portions of the LOTC appear to capture the unique similarity
679 of observed actions at the subordinate and basic level, with a preference for the basic level.
680 Together, our results offer new perspectives on the hierarchical organization of observed actions
681 and the neural basis of the basic level advantage.

682 **Figure captions**

683 **Figure 1. Top panel:** Stimulus set and corresponding hierarchical structure (based on Zhuang and
684 Lingnau, 2021). Left column: example stimuli (one out of six exemplars per subordinate action).
685 2nd-4th column: English labels of actions at the subordinate, basic and superordinate level. **Bottom**
686 **panel:** model RDMs for observed actions at the subordinate (left), basic (middle), and
687 superordinate (right) level. Each model RDM consists of a 72 x 72 matrix (12 actions, with 6
688 exemplars per action), where each cell in the matrix corresponds to the dissimilarity between a
689 pair of actions. Yellow: high dissimilarity, blue: low dissimilarity.

690
691 **Figure 2.** Stimulus selection and validation. **A.** Behavioral action space model, averaged across N=18
692 participants and across six exemplars per action. **B.** 2-dimensional representation of the results
693 shown in panel A, resulting from multidimensional scaling analysis (Borg and Groenen, 2005). For
694 color code see legend in panel C. The numbers refer to the twelve actions at the subordinate
695 level (1: 'to ride a motorbike', 2: 'to ride a bike', 3: 'to swim front crawl', 4: 'to swim backstroke', 5:
696 'to drink beer', 6: 'to drink water', 7: 'to eat an apple', 8: 'to eat cake', 9: 'to clean windows', 10:
697 'to brush teeth', 11: 'to do the dishes', and 12: 'to clean the face'. **C.** Dendrogram resulting from
698 hierarchical cluster analysis, confirming the clusters corresponding to the three superordinate
699 categories (locomotion, ingestion, cleaning) and the six basic level categories (see also Figure 1).

700
701 **Figure 3.** Experimental procedure used in the fMRI experiment. We used a rapid event-related
702 design, where each trial consisted of a static image (1 s) depicting one of the twelve actions (see
703 Table 1, 2nd column), followed by a fixation cross (3 s). During occasional catch trials (11 % of all
704 trials), participants had to perform a category verification task, targeting the action presented in
705 the previous trial. Questions to be answered during catch trials targeted the superordinate
706 (locomotion?), basic (to swim?) or subordinate (to swim breaststroke?) level with an equal
707 probability. Moreover, null events (22.2% of all trials) were included to enhance design efficiency
708 (see text for details).

709
710 **Figure 4.** Partial correlations between neural RDMs and the models corresponding to the three
711 taxonomic levels (see also Figure 1), regressing out a low-level visual control model, based on the
712 first convolutional layer of a deep neural network (ResNet50, He et al., 2015), trained on a large
713 scale image data set (ImageNet dataset) to distinguish image classes and a scene control model,
714 based on the second-to last layer of ResNet50, trained to distinguish between different scene
715 categories; Zhou et al., 2017 and 2018; see Section ROI-based RSA for details). Error bars show
716 the standard error of the mean. Asterisks illustrate statistical significance (*: $q_{FDR} < 0.05$, **: $q_{FDR} <$
717 0.01 , ***: $q_{FDR} < 0.005$) of one-sample t-tests against zero with FDR correction for all possible
718 combinations of taxonomic level and ROI. Since a 2-factorial (level x ROI) repeated measures
719 ANOVA revealed a significant interaction between taxonomic level and ROI, partial correlation
720 values between the three taxonomic levels within each ROI were compared using pairwise
721 comparisons (corrected for multiple comparisons using FDR).

722
723 **Figure 5.** Neural RDM (left panel) and the corresponding 2D visualization of the MDS results (right
724 panel) obtained in bilateral LOTC (A and B) and bilateral V1 (C and D) after regressing out the low-
725 level visual control model (based on the first convolutional layer of ResNet50, trained to
726 distinguish image classes) and the scene control model (based on the second-to last layer of
727 ResNet50, trained to distinguish between scene categories; Zhou et al., 2017 and 2018; see
728 Section ROI-based RSA for details), using the same ROIs as those shown in Figure 4. Colors to
729 indicate actions belonging to the three superordinate level categories (red-locomotion, blue-
730 ingestion, and green-cleaning) are the same as in Figure 2. Opened versus filled symbols indicate
731 different actions at the basic level, whereas circles versus squares are used to distinguish actions
732 at the subordinate level.

733

734 **Figure 6.** Results of the searchlight-based multiple regression RSA for the subordinate (left panel),
735 basic (middle panel) and superordinate (right panel) model. **A:** Multiple regression RSA,
736 regressing out the low-level visual control model and the scene control model (see section
737 Searchlight-based RSA for details). **B:** Multiple regression RSA, regressing out the low-level visual
738 control model, the scene control model and the remaining two taxonomic models. For group
739 statistics (N=23), beta weights resulting from the multiple regression RSA were entered into one-
740 sample t-tests against zero. The statistical t-value maps were corrected for multiple comparisons
741 using TFCE ($z > 1.65$, TFCE-corrected $p < .05$, one-tailed) as implemented in CoSMoMVPA
742 (Oosterhof et al., 2016).

743

744 **Figure 7.** Conjunction map for the unique representation of observed actions at the subordinate and
745 basic level (see Figure 6B). See text for details.

746

747 **Figure 8.** Brain areas capturing the representational space of actions obtained from behavioral
748 ratings (see Figure 2A). **A:** Brain areas capturing the behavioral dissimilarity structure after
749 regressing out the low-level visual control model and the scene control model. **B-D:** Brain areas
750 capturing the behavioral dissimilarity structure after regressing out the low-level visual control
751 model, the scene control model and models for the (B) subordinate, (C) basic and (D)
752 superordinate level. For the results of a control analysis examining the areas revealed by a whole-
753 brain searchlight RSA for the low-level visual control model, see Figure 8-1.

754

755 **Figure 8-1.** Results of the whole-brain searchlight RSA for the low-level visual control model. See
756 methods section for details.

757

758 **Tables**

759

760 **Table 1.** Overview Regions of Interest. 1st column: abbreviations used in the following figures (LH:
761 left hemisphere, RH: right hemisphere). 2nd column: peak MNI coordinates (identified based on the
762 RFX GLM contrast 'all actions vs. baseline'; see text for details). 3rd and 4th column: label and
763 anatomical atlas used for ROI selection.

ROIs	MNI 152			Label	Atlas
	X	Y	Z		
V1, LH	-14	-92	-4	visual cortex (V1 BA 17L)	Jülich Histological atlas
V1, RH	12	-90	0	visual cortex (V1 BA 17R)	Jülich Histological atlas
LOTc, LH	-42	-66	0	combination of inferior lateral occipital cortex and temporooccipital part	Harvard-Oxford Cortical structural
LOTc, RH	46	-74	0	combination of inferior lateral occipital cortex and temporooccipital part	Harvard-Oxford Cortical structural
SPL, LH	-30	-52	52	superior parietal lobule	Harvard-Oxford Cortical structural
SPL, RH	20	-56	52	superior parietal lobule	Harvard-Oxford Cortical structural
IPL, LH	-58	10	24	inferior parietal lobule (PFL)	Jülich Histological atlas
IPL, RH	62	-38	12	inferior parietal lobule (PFR)	Jülich Histological atlas
dPM, LH	-6	10	44	premotor cortex (BA6)	Jülich Histological atlas
dPM, RH	2	10	46	premotor cortex (BA6)	Jülich Histological atlas
IFG, LH	-40	10	24	inferior frontal gyrus pars opercularis	Harvard-Oxford Cortical structural
IFG, RH	44	6	24	inferior frontal gyrus pars opercularis	Harvard-Oxford Cortical structural

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Table 2. Peak locations for the three taxonomic levels in the whole-brain searchlight

		MNI 152			Labels of brain regions
		x	y	z	
Regressing out low-level visual control model and scene control model only	Subordinate level	31	-48	-9	R Temporal occipital fusiform cortex
	Basic level	36	-62	-6	R occipital fusiform cortex
	Superordinate level	30	-94	-4	R occipital pole
Regressing out low-level visual control model, scene control model and the other two models	Subordinate level	24	-58	-12	R Temporal occipital fusiform cortex
	Basic level	40	-62	-10	R occipital fusiform cortex
	Superordinate level	-	-	-	-

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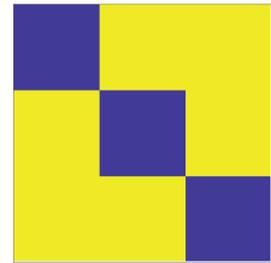
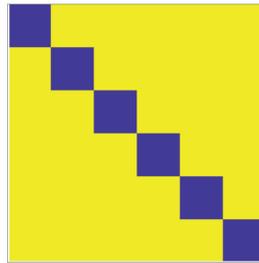
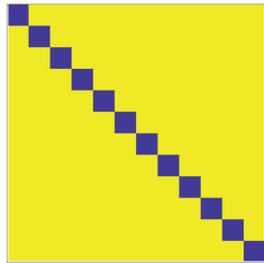
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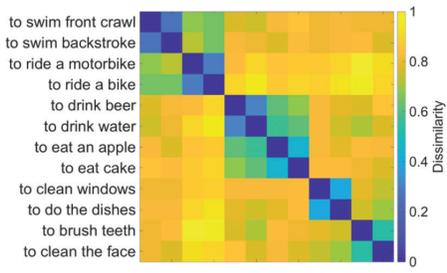
A

Stimuli	Subordinate level	Basic level	Superordinate level
	to ride a motorbike	to ride	locomotion
	to ride a bike		
	to swim front crawl	to swim	
	to swim backstroke		
	to drink water	to drink	ingestion
	to drink beer		
	to eat cake	to eat	
	to eat an apple		
	to clean windows	to do housework	cleaning
	to do the dishes		
	to brush teeth	to clean the body	
	to clean the face		

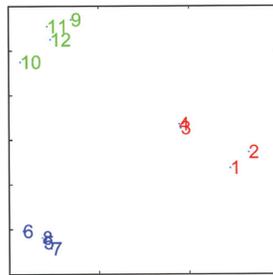
B



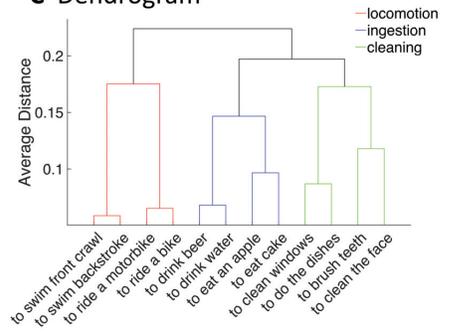
A Behavioral action space model

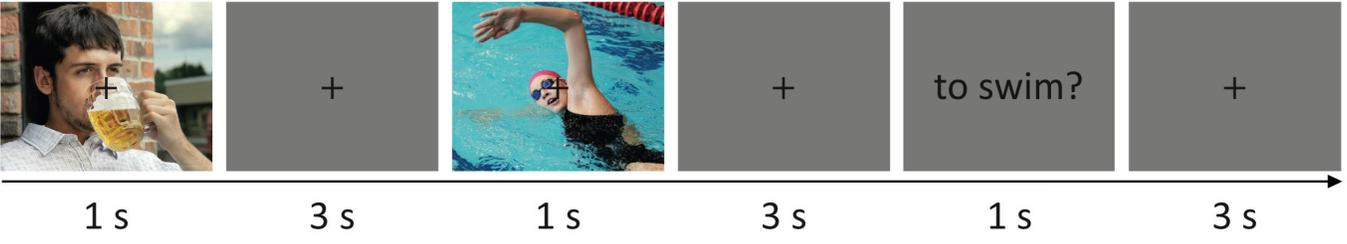


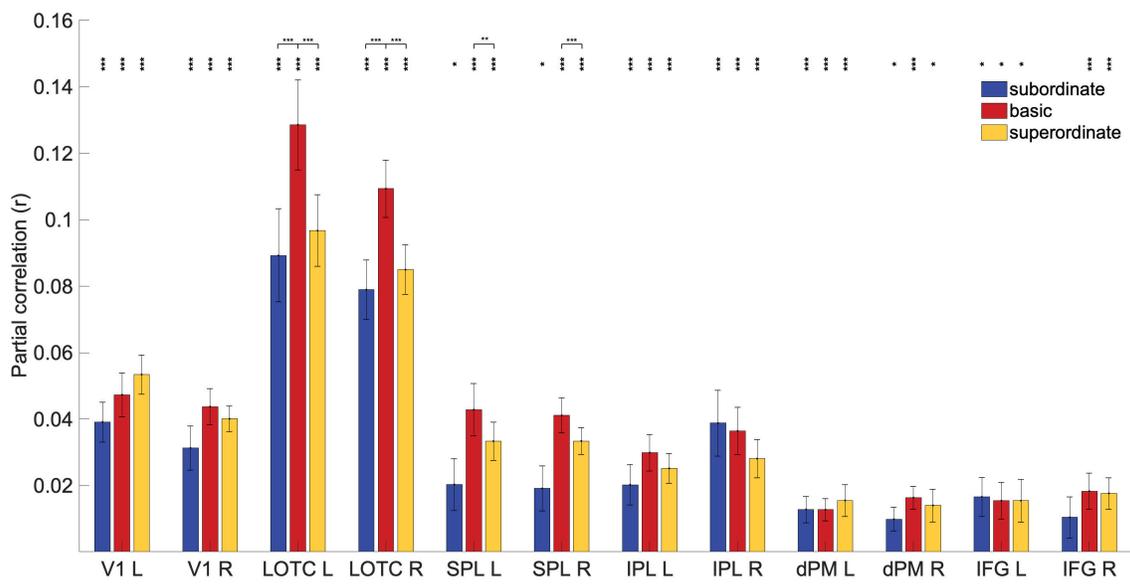
B 2D representation



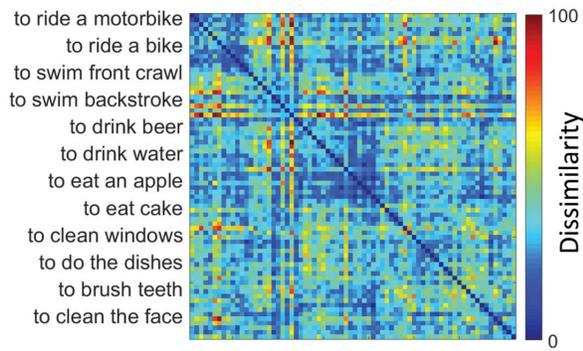
C Dendrogram



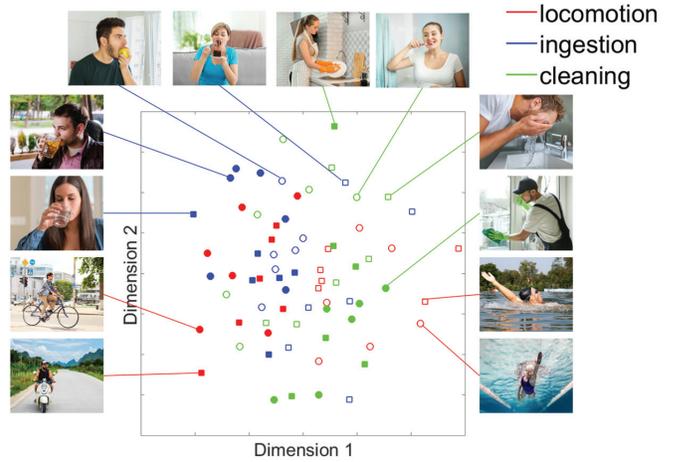




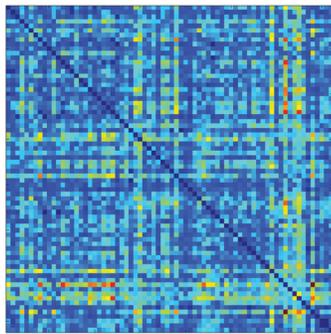
A Neural RDM (LOTC)



B 2D visualization (LOTC)



C Neural RDM (V1)



D 2D visualization (V1)

