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## Expert tool users show increased differentiation between visual representations of hands and tools

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1 **Title**

2 ***Expert tool users show increased differentiation between visual***  
3 ***representations of hands and tools***

4 **Abbreviated Title**

5 ***Expert tool users do not embody their hand-held tools***

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16

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25

26 **Abstract**

27 The idea that when we use a tool we incorporate it into the neural representation of our  
28 body (*embodiment*) has been a major inspiration for philosophy, science and  
29 engineering. While theoretically appealing, there is little direct evidence for tool  
30 embodiment at the neural level. Using functional magnetic resonance imaging (fMRI) in  
31 male and female human subjects, we investigated whether expert tool users (London  
32 litter pickers: n=7) represent their expert tool more like a hand (neural embodiment) or  
33 less like a hand (neural differentiation), as compared to a group of tool novices (n=12).  
34 During fMRI scans, participants viewed first-person videos depicting grasps performed  
35 by either a hand, litter picker or a non-expert grasping tool. Using representational  
36 similarity analysis, differences in the representational structure of hands and tools were  
37 measured within occipitotemporal (OTC). Contrary to the neural embodiment theory, we  
38 find that the experts group represent their own tool less like a hand (not more) relative  
39 to novices. Using a case-study approach, we further replicated this effect,  
40 independently, in 5 of the 7 individual expert litter pickers, as compared to the novices.  
41 An exploratory analysis in left parietal cortex, a region implicated in visuomotor  
42 representations of hands and tools, also indicated that experts do not visually represent  
43 their tool more similar to hands, compared to novices. Together, our findings suggest  
44 that extensive tool use leads to an increased neural differentiation between visual  
45 representations of hands and tools. This evidence provides an important alternative  
46 framework to the prominent tool embodiment theory.

47 **Significance Statement**

48 It is commonly thought that tool use leads to assimilation of the tool into the neural  
49 representation of the body, a process referred to as embodiment. Here, we demonstrate  
50 that expert tool users (London litter pickers) neurally represent their own tool less like a  
51 hand (not more), compared to novices. Our findings advance our current understanding  
52 for how experience shapes functional organisation in high-order visual cortex. Further,  
53 this evidence provides an alternative framework to the prominent tool embodiment  
54 theory, suggesting instead that experience with tools leads to more distinct, separable  
55 hand and tool representations.

56 **Introduction**

57 Experience using tools is commonly thought to lead to an integration between the  
58 neural representations of the body and the tool, a process known as *embodiment*  
59 (Maravita and Iriki, 2004). While theoretically appealing, there is little direct evidence for  
60 tool embodiment at the neural level. Previous research assessing tool embodiment,  
61 such as the influential work of Iriki and colleagues (Iriki et al., 1996), measured whether  
62 tool use affects the visual representation of hand-centered space [e.g. multisensory  
63 peripersonal space (Maravita and Iriki, 2004)]. However, this is an indirect measure of  
64 hand representation and is therefore open to alternative interpretations (Holmes, 2012).  
65 Additionally, a more recent tool embodiment approach using electroencephalography  
66 (EEG) examined how tactile information carried by a hand-held tool is processed by the  
67 somatosensory system as compared to the hand itself (Miller et al., 2019). But  
68 considering that the tool is held by the hand, it is not clear if this low-level representation  
69 is actually attributable to the tool, or more likely – to the mechanoreceptors in the hand  
70 that mediate this information. As such, there is still not a strong proof of concept in the  
71 literature that tool use leads to sensory embodiment.

72

73 Here, we used fMRI brain decoding to directly quantify similarities between visual  
74 representations of hands and tools in expert tool users and novices. We studied  
75 individuals with extensive experience using a litter picking tool (expert tool users) as  
76 well as a group of novice litter picker users. We specifically chose to study expert tool  
77 users, based on the assumption that the extensive tool use of the experts would make  
78 them most likely to embody their tools. During fMRI scans, participants viewed first-

79 person videos depicting grasps performed by either a hand, litter picker or a non-expert  
80 grasping tool (tongs). Using representational similarity analysis, differences in the  
81 representational structure across hands and tools were measured within  
82 occipitotemporal cortex (OTC). We specifically focused on OTC because it contains  
83 spatially overlapping, but distinct, representations for hands and tools (Bracci et al.,  
84 2012). OTC has also been closely linked in visuomotor (Orlov et al., 2010) and  
85 multisensory hand representations (Gentile et al., 2013), and has also been associated  
86 with hand embodiment under the rubber hand illusion (Limanowski et al., 2014). As  
87 such, it provides a perfect test bed for investigating tool embodiment. Additionally, to  
88 test whether a different result would potentially be observed within neural structures  
89 directly implicated in motor planning and execution for hand- and tool-use (Gallivan et  
90 al., 2013), an exploratory analysis was performed in left parietal cortex. We focused on  
91 the left hemisphere because motor planning/tool-use has been shown to be left-  
92 lateralised in parietal cortex (Brandi et al., 2014; Gallivan and Culham, 2015).

93

94 Under the theoretical framework that defines neural embodiment as the successful  
95 integration of brain resources typically devoted to control the body to represent and  
96 operate external objects [e.g. tools, prosthetic limbs; (de Vignemont, 2011; Makin et al.,  
97 2017)], we proposed three predictions for what we might observe: (i) experts could  
98 represent the expert tool more like a hand compared to novices, i.e., neural  
99 embodiment, (ii) experts could represent the expert tool less like a hand compared to  
100 novices, i.e., neural differentiation or (iii) experts could show no differences compared to  
101 novices (Fig. 1A). Interestingly, we found that, contrary to the neural embodiment

102 theory, expert tool users represent the expert tool less like a hand, i.e., greater neural  
103 *dissimilarity* between the visual representations of the expert tool and hands within  
104 OTC, compared to the novices. Using Crawford & Howell's (1998) method, a modified t-  
105 test, we independently replicated this effect in 5 of 7 individual expert litter pickers, as  
106 compared to the novices. Further, we found that this result could not be explained by  
107 the low-level representational structure captured in primary visual cortex. An exploratory  
108 analysis in left parietal cortex revealed a similar pattern as OTC. These findings provide  
109 a novel framework for how tool use shapes the representational structure of hands and  
110 tools, such that extensive tool use leads to a more distinct tool representation, as  
111 compared to the hand, throughout the visuomotor network. Collectively, this evidence  
112 provides an important alternative framework to the tool embodiment theory.

113

#### 114 **Methods**

##### 115 *Participants*

116 To identify 'expert' litter pickers, recruitment adverts were distributed with multiple  
117 relevant individuals/groups: sanitation supervisors stationed in London Underground  
118 stations (e.g. King's Cross St. Pancras, Westminster, Camden, Russell Square etc.),  
119 Heads of Parks and Sanitation at several UK city councils (e.g. Islington, Camden,  
120 Brighton and Hove), and with several volunteer litter picking organizations: Keep Britain  
121 Tidy, Litter Action, CleanupUK, Helping Hand Environmental and the Dorset Devils.  
122 From these adverts, 52 respondents were screened via a telephone interview or online  
123 survey. From this group, 13% of respondents [n=7; mean age (SD) = 47 (8.11), 4  
124 females, all right-handed, mean years of education (SD) = 15.9 (1.57)] were invited to

125 participate in the study, based on their litter picking usage being above a minimum  
 126 threshold (composite score of their *previous* litter picking use and their *current* litter  
 127 picking usage) and compatibility with MRI safety regulations. We also recruited a group  
 128 of novices matched in age [ $n=15$ ; mean age (SD) = 43 (7.39), 3 females, 1 left-handed,  
 129 mean years of education (SD) = 14.8 (1.86)]. All participant demographics are reported  
 130 in Table 1. Recruitment was conducted in accordance with University College London's  
 131 research ethics committee (Ref: 9937/001). Informed consent and consent to publish  
 132 was obtained in accordance with ethical standards of the Declaration of Helsinki  
 133 (1964). Three novices were excluded from fMRI data analysis because they did not  
 134 complete all of the functional runs, due to feelings of anxiety and claustrophobia.

135

136 *Litter picking usage measurements*

137 Participants were asked to estimate their frequency of using a litter picking on a weekly  
 138 and daily basis, as well as to estimate how long they've been using a litter picker. Litter  
 139 picking usage habits are summarized below in Table 1. Participants were not asked to  
 140 report their previous experience with the non-expert tool (tongs).

SUBJECT	GENDER	AGE	YEARS OF EDUCATION	LITTER PICKER USAGE	YEARS LITTER PICKING
EXP01	F	53	19	2.5 days/week (1.5 hr/day)	1.5
EXP02	M	53	15	4.5 days/week (1.5 hr/day)	10
EXP03	M	46	15	4 days/week (1.5 hr/day)	.5
EXP04	F	47	15	1.5 days/week (2 hr/day)	6
EXP05	M	56	15	1 day/week (1 hr/day)	3
EXP06	F	36	17	7 days/week (2.5 hr/day)	2
EXP07	F	36	15	3.5 days/week (1 hr/day)	4

141 **Table 1. Participant demographics.** Expert litter pickers (EXP).

142

143 *Experimental design*

144 *fMRI task stimuli.* For the main functional task, participants viewed first-person videos of  
145 grasping actions being performed using three different effector categories: hands, litter  
146 pickers (expert tool) and tongs (non-expert tool). The stimuli included 48 unique videos.  
147 Of the 48 videos, there were 16 videos for each effector category. Half of the videos (8  
148 per effector) were presented as left-handed and the other half as right-handed. For the  
149 8 videos for each effector category, videos varied in multiple features: scene context  
150 [common scenes typical for hand or tool actions: street (tool), grass (tool), kitchenette  
151 (hand), desk (hand)], as well as the size of the object being grasped (small vs. large; for  
152 example, a small object used was a train ticket and a large object used was a tennis  
153 ball; to access all of the videos see <https://osf.io/p4q3y/>). A fourth effector, prosthetic  
154 hands, was also included in the design. However, this condition was included as part of  
155 a separate study involving amputee participants.

156

157 Separately, for the functional localizer scan, participants viewed videos of tools, hands,  
158 and two types of control categories: objects and low-level visual control stimuli (to  
159 access the full functional localizer video see <https://osf.io/p4q3y/>).

160

161 *fMRI task design.* For the main functional task, the presentation of the stimuli was  
162 counter-balanced across the 4 functional runs, to best control for pairwise order effects.  
163 Each functional run was 7 min 26 s in length. Within each run, each video was

164 presented once. Each video was displayed for 3.0 s, followed by 2.5 s of a red fixation  
165 point against a grey background. Additionally, catch trials were introduced to keep  
166 subjects engaged throughout the scan, where an image of a leprechaun face would  
167 randomly appear on the center of the screen. Participants were instructed (prior to  
168 starting the task) to wiggle their toes whenever a leprechaun face appeared. These  
169 trials were modelled separately and excluded from further analyses. The videos were  
170 constructed using MoviePy, a python package for video editing  
171 (<https://zulko.github.io/moviepy/>). Stimuli were presented on a screen located at the rear  
172 end of the MRI scanner and were viewed through a mirror mounted on the head coil.  
173 The videos were presented via VLC player (<https://www.videolan.org/vlc/>) on a Dell  
174 Latitude laptop.

175

176 For the functional localizer scan, participants were instructed to maintain fixation upon a  
177 cross in the centre of the screen that was visible throughout the experiment. The  
178 localizer run began and ended with a 20 s fixation baseline, followed by five  
179 experimental blocks of five 21 s blocks (four experimental blocks and one baseline  
180 block), ending with another 20 s fixation baseline (for a total run duration of 9 min, 20 s).  
181 The order of blocks was semi-counterbalanced across the five sets. Each block of the  
182 video conditions was comprised of three videos of 7 s each, with each video depicting a  
183 different exemplar of the condition.

184

185 *MRI data acquisition*

186 The MRI measurements were obtained using a 3-Tesla Quattro scanner (Siemens,  
187 Erlangen, Germany) with a 32-channel head coil. Anatomical data were acquired using  
188 a T1-weighted magnetization prepared rapid acquisition gradient echo sequence  
189 (MPRAGE) with the parameters: TR = 2.54 s, TE = 3.34 ms, FOV = 256 mm, flip angle  
190 = 7°, and voxel size = 1 mm isotropic resolution. Functional data based on the blood  
191 oxygenation level-dependent signal were acquired using a multiband gradient echo-  
192 planar T2\*-weighted pulse sequence (Uğurbil et al., 2013) with the parameters: TR =  
193 1.5 s, TE = 35 ms, flip-angle = 70°, multi-band acceleration factor = 4, FOV = 212 mm,  
194 matrix size of 106 x 106, and voxel size = 2 mm isotropic resolution. Seventy-two slices,  
195 with a slice thickness of 2 mm and no slice gap, were oriented in the anterior  
196 commissure – posterior commissure, covering the whole cortex, with partial coverage of  
197 the cerebellum. Each of the four functional runs comprising the main task consisted of  
198 298 volumes (7 min 26 s). For the functional localizer, there was one functional run  
199 consisting of 374 volumes. For all functional scans, the first dummy volume of every run  
200 was saved and later used as a reference for co-registration.

201

#### 202 *fMRI analysis*

203 Functional MRI data processing was carried out using FMRIB's Expert Analysis Tool  
204 (FEAT; Version 6.0), part of FSL (FMRIB's Software Library, [www.fmrib.ox.ac.uk/fsl](http://www.fmrib.ox.ac.uk/fsl))  
205 and Connectome Workbench ([humanconnectome.org](http://humanconnectome.org)) software, in combination with  
206 Matlab scripts (R2019b, v9.7, The Mathworks Inc, Natick, MA), both developed in-house  
207 [including an FSL-compatible RSA toolbox (Nili et al., 2014)] and as part of the RSA  
208 Toolbox (Wesselink and Maimon-Mor, 2018).

209

210 *fMRI pre-processing*

211 Registration of the functional data to the high-resolution structural image was carried out  
212 using the boundary-based registration algorithm (Greve and Fischl, 2009). Registration  
213 of the high resolution structural to standard space images was carried out using FLIRT  
214 (Jenkinson and Smith, 2001; Jenkinson et al., 2002) and was then further refined using  
215 FNIRT nonlinear registration (Andersson et al., 2007b, 2007a). The following pre-  
216 statistical processing was applied; motion correction using MCFLIRT (Jenkinson et al.,  
217 2002); non-brain removal using BET (Smith, 2002); spatial smoothing using a Gaussian  
218 kernel of FWHM 3mm for the functional task data and 5mm for the functional hand-tool  
219 localizer; grand-mean intensity normalisation of the entire 4D dataset by a single  
220 multiplicative factor; high-pass temporal filtering (Gaussian-weighted least-squares  
221 straight line fitting, with  $\sigma=50s$ ). Further, to minimize potential biases from individual  
222 runs, the functional data across the individual runs was aligned to a functional mid-  
223 space using FMRIB's Linear Image Registration Tool [FLIRT (Jenkinson and Smith,  
224 2001; Jenkinson et al., 2002)]. This functional mid-space was later used to align the  
225 parameter estimates and residuals, from each run, to the same functional space for the  
226 representational similarity analysis.

227

228 *Low level task-based analysis*

229 We applied a general linear model (GLM) as implemented in FEAT, to each functional  
230 run. For the main analysis, left and right-handed versions of the same videos were  
231 modelled together against rest (fixation). Time-series statistical analysis was carried out

232 using FILM with local autocorrelation correction (Woolrich et al., 2001). The time series  
233 model included trial onsets convolved with a double gamma HRF function; six motion  
234 parameters were added as confound regressors. Trials for each video condition were  
235 modelled separately, except left- and right-handed videos were modelled together.  
236 Indicator functions were added to model out single volumes identified to have excessive  
237 motion (>1mm). A separate regressor was used for each high motion volume, no more  
238 than 8 volumes were found for an individual run (2.1% of the entire run). Additionally, in  
239 the supplementary analysis exploring the effects of video laterality, videos were  
240 modelled separately for each effector category and whether they were left-handed or  
241 right-handed against rest (fixation) and averaged across the other features (context and  
242 object size). We further used this analysis to confirm our main analysis for group  
243 differences in *effector category distances*.

244

245 For the functional localizer scan, a single contrast for the conditions of interest were  
246 defined as hands + tools > objects + low level visual stimulus. The activity patterns  
247 associated with this contrast were then used to define functional regions of interest  
248 (ROIs).

249

250 For each participant, parameter estimates of the different effector categories and GLM  
251 residuals of all voxels within the ROI were extracted from each run's first-level analysis.  
252 For each participant, the parameter estimates and GLM residuals from each run were  
253 then aligned to the functional mid-space using FMRIB's Linear Image Registration Tool

254 [FLIRT (Jenkinson and Smith, 2001; Jenkinson et al., 2002)]. The subsequent RSA  
255 analysis was conducted within this functional mid-space.

256

257 *Defining regions of interest (ROIs)*

258 *Occipitotemporal cortex.* Using functional MRI data collected from a separate,  
259 independent group of controls (n=20) that viewed the same functional hand-tool  
260 localizer (described above), a whole brain group activation map for the contrast hands  
261 and tools over moving objects and low-level visual stimulus was constructed. This group  
262 map revealed a large cluster covering OTC (z-threshold of 3.1). This cluster was  
263 isolated, binarized and registered to the functional space of the functional localizer scan  
264 using FLIRT. Since the focus of the study was on identifying hand and tool selective  
265 voxels within occipitotemporal cortex (OTC), the analysis was restricted to individually  
266 defined ROIs within this large OTC map defined by the independent group of controls.  
267 Using the functional localizer data, for each participant in the present study, a hand and  
268 tool selective region of interest (ROI) within the large OTC map was defined by  
269 selecting the top 100 voxels in each hemisphere showing the strongest greatest  
270 preference to videos of hands and tools over moving objects and low level visual  
271 stimulus for each participant. In total, the OTC region of interest included 200 voxels:  
272 100 in the left hemisphere and 100 in the right hemisphere. These individually defined  
273 ROIs were then transformed from the functional space of the functional localizer scan to  
274 the functional mid-space of the functional task scans (described above).

275

276 *Primary visual cortex (V1)*. The primary visual cortex region of interest was derived from  
277 the Juelich Histological Atlas' (GM Visual Cortex V1 BA17 L and R) maximum  
278 probabilistic map (unthresholded). Each V1 hemisphere ROI was binarized and  
279 transformed from MNI space to the functional space of the functional localizer scan  
280 using FLIRT. To identify visually active voxels within each ROI, using the independent  
281 hand-tool functional data, the top 100 most activated voxels, in each hemisphere, were  
282 selected based on the contrast of all video conditions > baseline. In total, the V1 ROI  
283 included 200 voxels: 100 in the left hemisphere and 100 in the right hemisphere. These  
284 individually defined ROIs were then transformed from the functional space of the  
285 functional localizer scan to the functional mid-space of the functional task scans. ROIs  
286 from all participants were superimposed (Fig. 3A).

287

288 *Left parietal cortex*. As an exploratory analysis, the analysis performed in OTC was  
289 conducted in left parietal cortex. Using the functional MRI data collected from the  
290 separate, independent group of controls (n=20) that viewed the same functional hand-  
291 tool localizer (described above for OTC), a whole brain group activation map for the  
292 contrast hands and tools over moving objects and low level visual stimulus was  
293 constructed. This group map revealed a large cluster covering parietal cortex (z-  
294 threshold of 3.1). The left parietal cortex cluster was isolated, binarized and registered  
295 to the functional space of the functional localizer scan using FLIRT. Since the focus of  
296 the study was on identifying hand and tool selective relevant voxels, the analysis was  
297 restricted to individually defined ROIs within the large left parietal map. To identify hand  
298 and tool selective voxels within this map, the top 200 most activated voxels within the

299 left parietal hand-tool conjunction map were selected, for each participant, based on a  
300 hands + tools > objects + low level visual stimulus contrast. These individually defined  
301 ROIs were then transformed from the functional space of the functional localizer scan to  
302 the functional mid-space of the functional task scans. ROIs from all participants were  
303 superimposed (Fig. 3C).

304

#### 305 *Representational similarity analysis (RSA)*

306 To assess the hand-tool representation structure within the ROI, we utilised a  
307 multivariate approach, representational similarity analysis, where pairwise  
308 representational dissimilarity distances between individual videos were calculated  
309 (Diedrichsen and Kriegeskorte, 2017). For each participant, parameter estimates of the  
310 individual videos and GLM residuals of all voxels within the ROI were extracted from  
311 each run's first-level analysis. To increase the reliability of the distance estimates,  
312 parameter estimates underwent multi-dimensional normalization based on the voxels'  
313 covariance matrix calculated from the GLM residuals. This was done to ensure that  
314 parameter estimates from noisier voxels will be down-weighted (Walther et al., 2016).  
315 Cross-validated (leave-one-run-out) Mahalanobis distances (also known as LDC –  
316 linear discriminant contrast (Nili et al., 2014; Walther et al., 2016) were then calculated  
317 between each pair of videos. Analysis was run on adapted version of the RSA toolbox in  
318 Matlab (Nili et al., 2014), customized for FSL (Wesselink and Maimon-Mor, 2018).

319

320 For OTC, this analysis was performed separately for each participant and ROI (left  
321 OTC, right OTC), resulting in pairwise dissimilarity distance values comparing each

322 video condition (note that left- and right-handed videos were modelled together in this  
323 analysis). These distance values for each ROI were inputted into a mixed level analysis  
324 of variance (described later in statistical analyses). Due to no significant interaction with  
325 ROI (left OTC, right OTC), the resulting values for left and right OTC were averaged for  
326 each participant, for visualization purposes. These distance values were then depicted  
327 as a representational dissimilarity matrix (RDM), where each element in the RDM  
328 corresponds to a single pairwise dissimilarity distance value. The group RDMs (Fig. 2A)  
329 were constructed through averaging each pairwise distance element in the matrix of  
330 each participant for each group (novices, experts). Additionally, multidimensional  
331 scaling plots (to access see <https://osf.io/p4q3y/>) were derived from these group RDMs.  
332 MDS projects the higher-dimensional RDM into a lower (2D) dimensional space. Note  
333 that MDS is presented for intuitive visualisation purposes only and was not used for  
334 statistical analysis. For primary visual cortex, the same analysis parameters were used,  
335 except the RSA was performed across both hemispheres. For parietal cortex, the same  
336 analysis parameters for OTC were used, except we only analysed the left hemisphere.

337

338 For the laterality RSA analysis, the analysis was performed twice: separately for the  
339 average parameter estimates for left- and right-handed stimuli. Cross-validated (leave-  
340 run-out) Mahalanobis distances were calculated between the parameter estimates for  
341 each pair of conditions (e.g. for left-handed stimuli: left-handed hands, left-handed litter  
342 pickers, left-handed tongs). Specifically, for the laterality analysis performed in OTC,  
343 this was done separately in each OTC hemisphere for each participant, resulting in 4  
344 RDMs: left-handed stimuli in left OTC, right-handed stimuli in left OTC, left-handed

345 stimuli in right OTC, right-handed stimuli in right OTC. The group RDMs for each of  
346 these brain regions were constructed through averaging each pairwise distance element  
347 in the 3x3 matrix of each participant for each group (novices, experts). Again, for  
348 parietal cortex, the same analysis parameters for OTC were used, except we only  
349 analysed the left hemisphere (i.e. no within subject-factor of ROI in the mixed-model  
350 ANOVA).

351

### 352 *Statistical analyses*

353 All statistical testing was performed using IBM SPSS Statistics for Macintosh (Version  
354 24), with the exception of the Bayesian analysis which was run on JASP [Version 0.11.1  
355 (Jasp Team, 2019)] Tests for normality were carried out using a Shapiro Wilk test. For  
356 statistical analyses of RSA measures in OTC, a mixed level analysis of variance  
357 (ANOVA; after testing for normality using the Shapiro-Wilks test,  $p > .05$ ) was performed  
358 with the within-subject factors: *effector category distances* (hands ↔ litter pickers, hand  
359 ↔ tongs, litter pickers ↔ tongs) and *region of interest* (left OTC, right OTC) and a  
360 between subject factor *group* (novices, experts). For the secondary OTC analysis that  
361 controlled for low level representational structure captured in primary visual cortex, the  
362 same parameters for the OTC mixed level ANOVA described above were used,  
363 however the average *effector category* distance outputted from primary visual cortex for  
364 each participant was used as a covariate. For primary visual cortex, a mixed level  
365 analysis of variance (ANOVA; after testing for normality using the Shapiro-Wilks test,  
366  $p > .05$ ) was performed with the within-subject factors: *effector category distances* (hands  
367 ↔ litter pickers, hand ↔ tongs, litter pickers ↔ tongs) and a between subject factor

368 *group* (novices, experts). For the OTC laterality analysis, each participant's cross-  
369 *effector category* distances from each of the 2 RDMs for each ROI (left OTC, right OTC)  
370 were inputted into a mixed level ANOVA (after testing for normality using the Shapiro-  
371 Wilks test,  $p > .05$ ) was performed with the within-subject factors included: *effector*  
372 *category distances* (hands ↔ litter pickers, hand ↔ tongs, litter pickers ↔ tongs),  
373 *laterality* (left- or right-handed) and *region of interest* (left OTC, right OTC) and a  
374 between subject factor *group* (novices, experts).

375

376 For the left parietal cortex RSA analyses, the same ANOVA parameters were used as  
377 OTC, except there was no within-subject factor of ROI. Within all of the above analyses,  
378 to explore the group differences in pairwise *effector category distance* pairs, two-tailed  
379 independent samples t tests and two-tailed Bayesian independent samples t tests were  
380 performed. The Cauchy prior width was set at 0.707 (default; Keysers et al., 2020). We  
381 interpreted the test based on the well accepted criterion of Bayes factor smaller than 1/3  
382 (Dienes, 2014) as supporting the null hypothesis. The strength of evidence was  
383 interpreted based on the classification provided in (Jeffreys, 1961), where a Bayes  
384 Factor above 10 (or below 0.1) is considered as strong evidence. Additionally, as an  
385 exploratory analysis to characterize the supporting evidence for tool embodiment in left  
386 parietal cortex, one-tailed Bayesian independent samples t tests were performed. The  
387 alternative hypothesis was defined as '*experts have smaller dissimilarity distances*  
388 *between hands and the expert tool (litter pickers) than novices*', i.e., *novices > experts*.

389

390 To test whether an individual expert litter picker's hands ↔ litter pickers distance was  
391 significantly different from the novices, we used Crawford & Howell's (1998) method  
392 which provides a point estimate of the abnormality of the individual case's distance from  
393 a control sample, as well as a confidence interval of the uncertainty associated with the  
394 point estimate (Crawford and Howell, 1998). To account for inter-individual differences  
395 not directly related to hand-tool representation, we first subtracted each participant's  
396 hands ↔ litter pickers distance by their litter pickers ↔ tongs distance. The analysis  
397 was performed using the Singlims.exe program (Crawford and Garthwaite, 2002).

398

### 399 **Results**

400 First, to investigate if experience with a hand-held tool leads to tools being *embodied*,  
401 we recruited individuals with extensive experience using a litter picking tool (n=7,  
402 identified from 52 screened litter pickers; see participant demographics in Table 1). To  
403 quantify whether the expert litter pickers neurally *embody* the litter picker, we used fMRI  
404 in combination with representational similarity analysis (RSA) to measure differences in  
405 the representational structure of hands and tools. During fMRI scans, participants  
406 viewed first-person videos of grasping actions being performed by three effector  
407 categories: hands, litter pickers (expert tool) and tongs (non-expert tool). Videos were  
408 visually matched across the effector categories. Videos also varied in multiple features:  
409 scene context [common scenes typical for hand or tool actions: street (tool), grass  
410 (tool), kitchenette (hand), desk (hand)], object sizes (small, large) and the laterality of  
411 stimuli (left- or right-handed; for screenshots of the videos, see Fig. 1B). Next,  
412 individualized hand and tool selective regions of interest (ROIs) within occipitotemporal

413 cortex were independently localised for each participant by choosing the 100 OTC  
414 voxels in each hemisphere showing the strongest preference to videos of hands and  
415 tools over moving objects and low-level visual stimulus (Fig. 1C).

416

417

**[INSERT FIGURE 1]**

418

419 **Expert tool users show increased differentiation between hands and tools in**  
420 **occipitotemporal cortex**

421 To calculate group differences between activation patterns for hands and tools in OTC,  
422 we first computed the representational dissimilarity distances comparing each of the  
423 video conditions to every other video condition (see Fig. 2A for the representational  
424 dissimilarity matrices for each group). While participants viewed multiple video  
425 conditions for each of the three effector categories, we focused on the representational  
426 distances between effector representations, across the multiple conditions. To do this,  
427 we averaged the cross-effector category representational dissimilarity distances for  
428 each participant. This resulted in three distances per participant, one for each cross-  
429 effector category pair (hands ↔ litter pickers, hands ↔ tongs, litter pickers ↔ tongs).  
430 We entered these distances into a mixed level ANOVA: within-subject factors included  
431 the three *cross-effector category distances* and *region of interest (ROI: left OTC, right*  
432 *OTC)*, with a between-subject factor of *group* (experts, novices). This analysis revealed  
433 a significant two-way interaction between the *effector category distances* and *group*  
434 [ $F_{(2,16)} = 17.495$ ,  $p < .001$ ;  $BF_{incl} = 72.313$ ; the three-way interaction between *region of*  
435 *interest, effector category distances* and *group* was not significant:  $F_{(2,16)} = 1.267$ ,  $p =$

436 .309;  $BF_{incl} = 1.088$ ; see Fig. 2B]. This suggests that there are group differences in the  
437 representational structure (full statistical report can be accessed at <https://osf.io/p4q3y/>).  
438 Specifically, expert tool users represented the expert tool less like hands, i.e., experts  
439 showed increased dissimilarity distances between the expert tool (litter picker) and  
440 hands, compared to the novices ( $t(17)=-3.385$ ,  $p = .004$ , two-tailed;  $BF_{10} = 11$ ). Thus,  
441 the extensive tool use of the experts leads to the visual representation of the tool to  
442 become more dissimilar to hands (not more similar). Moreover, this shift was also  
443 observed for the non-expert tool (tongs) with experts representing the tongs less like  
444 hands, i.e., experts showed increased dissimilarity distances between tongs and hands,  
445 compared to novices ( $t(17)=-2.574$ ,  $p = .020$ , two-tailed;  $BF_{10} = 3.1$ ). Additionally, the  
446 two grasping tools (litter pickers ↔ tongs) were represented equally similar to each  
447 other, i.e., no significant group differences in dissimilarity distances between the litter  
448 picker and tongs ( $t(17)=1.202$ ,  $p = .246$ , two-tailed;  $BF_{10} = 0.6$ ).

449

450

**[INSERT FIGURE 2]**

451

452 Considering the small sample size of the expert litter pickers group, we next sought to  
453 test whether the observed effect in the experts could be replicated in each individual  
454 expert litter picker, as compared to the novice group. As such, one could consider each  
455 expert litter picker to be a case study and an independent replication of the effect. To  
456 test this, we used Crawford & Howell's (1998) method (a modified t-test) to test whether  
457 each expert litter pickers' hands ↔ litter pickers distance was significantly different from  
458 the novices (Crawford and Howell, 1998). This analysis revealed that 5 of 7 expert litter

459 pickers showed significantly greater hands ↔ litter pickers distances (normalized by the  
460 litter pickers ↔ tongs distance), as compared to the novices (two-tailed; range of  $p$ -  
461 values for the 5 experts with significant tests:  $.002 < p < .022$ ;  $p$ -values for the 2 experts  
462 with non-significant tests:  $.144$  &  $.245$ ). This analysis further confirms that expert litter  
463 pickers show increased neural differentiation between visual representations of hands  
464 and tools within OTC.

465

466 To understand if the group differences in effector category distances observed in OTC  
467 are driven by differences in the low-level representational structure (e.g. potential  
468 differences in eye movements between experts and novices), we repeated the group  
469 analysis within a second ROI, primary visual cortex, as a control. This analysis revealed  
470 no significant *group* differences in *effector category distances* within primary visual  
471 cortex ( $F_{(2,17)} = .013$ ,  $p = .987$ ;  $BF_{incl} = .330$  Fig. 3B). However, qualitatively, we  
472 observed a trend for a main effect of *group* ( $F_{(1,17)} = 2.662$ ,  $p = .121$ ;  $BF_{incl} = 0.592$ ) with  
473 greater distances in the experts (full statistical report can be accessed at  
474 <https://osf.io/p4q3y/>). Despite not being significant, to highlight that the group  
475 differences within OTC are not driven by greater distances in the experts' low level  
476 representational structure captured within primary visual cortex, we included the  
477 average effector category distance in primary visual cortex for each participant as a  
478 covariate in the OTC analysis. Even when controlling for this low level representational  
479 structure, we still find significant *group* differences in *effector category distances* in OTC  
480 [significant interaction between *effector category distances*\**group*:  $F_{(2,17)} = 11.982$ ,  $p =$   
481  $.001$ ;  $BF_{incl} = 61.216$ ; full statistical report can be accessed at <https://osf.io/p4q3y/>].

482

483 Finally, we considered whether a neural embodiment result (i.e. tools becoming more  
484 similar to hands with extensive use) might be observed depending on the laterality of  
485 the presented stimuli (left- or right-handed), especially considering the experts reported  
486 only using the litter picker with their right hand. To test this, the previous RSA approach  
487 was repeated in OTC, except this time the video conditions were grouped by their  
488 laterality: left- or right-handed, i.e., averaged across other video conditions (group  
489 laterality RDMs available at <https://osf.io/p4q3y/>). Nonetheless, we did not observe a  
490 significant three-way interaction with the *laterality of the stimuli*, *group* and *effector*  
491 *category distances* [ $F_{(2,16)} = .043$ ,  $p = .958$ ;  $BF_{\text{incl}} = .039$ ], suggesting that the greater  
492 distances between hands and tools in the experts is not specific to the way in which the  
493 tool is visually experienced in the real world.

494

495

**[INSERT FIGURE 3]**

496

#### 497 **Investigating tool embodiment beyond occipitotemporal cortex**

498 While our experiment was specifically designed to leverage the known hand-tool  
499 representational relationship of OTC, our video stimuli also activated other regions  
500 relating to motor control and planning, providing us the opportunity to perform further  
501 exploratory analyses beyond OTC. To test whether a tool embodiment result would  
502 potentially be observed within neural structures involved more directly in motor planning  
503 for tool-use, an exploratory analysis was performed in left parietal cortex. This analysis  
504 revealed significant *group* differences in *effector category distances* [interaction

505 between *group\*effector category distances*:  $F_{(2,16)} = 5.058$ ,  $p = .020$ ;  $BF_{incl} = 1.139$ ; Fig.  
506 3D], similar to the interaction reported for OTC. However, the group comparisons  
507 between each individual *effector category distance* pair did not reach significance [hand  
508  $\leftrightarrow$  litter picker:  $t(18) = -.602$ ,  $p = .555$ , two-tailed;  $BF_{10} = 0.4$ ; hand  $\leftrightarrow$  tongs:  $t(18) =$   
509  $.440$ ,  $p = .116$ , two-tailed;  $BF_{10} = 1$ ; litter picker  $\leftrightarrow$  tongs:  $t(18) = -.824$ ,  $p = .421$ , two-  
510 tailed;  $BF_{10} = 0.5$ ]. Though, on average, experts showed greater distances between  
511 hands and litter pickers and hand and tongs compared to novices, similar to what we  
512 see within OTC. To verify there is no evidence supporting a neural embodiment result  
513 within parietal cortex that contradicts the result within OTC, a one-tailed Bayesian t test  
514 provided substantial evidence in support of the null hypothesis ( $BF_{10} = 0.2$ ), i.e., that on  
515 average experts do not visually represent an expert tool more similar to hands  
516 compared to the novices. Together, while the findings in parietal cortex are weaker than  
517 OTC, they are suggestive of a similar pattern and don't provide any evidence supporting  
518 tool embodiment.

519

## 520 Discussion

521 Here, a fMRI brain decoding technique was used to investigate how similar the  
522 representation of a hand is compared to an extensively used tool. This approach  
523 allowed us to directly compare hand and tool representations (independent of each  
524 other). Contrary to the tool embodiment theory, our findings show that expert tool users  
525 do not represent their own tool more similarly to a hand. Instead, experts showed  
526 greater dissimilarity distances between visual representations of hands and tools in  
527 occipitotemporal cortex (OTC). Further, using Crawford & Howell's (1998) method, we

528 independently replicated this effect in 5 of 7 individual expert litter pickers, as compared  
529 to the novices. Additionally, these group differences were not driven by potential  
530 differences in the low-level representation structure, as captured within primary visual  
531 cortex. Despite the experts reporting only using the litter picker with their right hand, we  
532 did not find that the group difference in dissimilarity distances between hands and the  
533 expert tool was specific to whether the expert tool was viewed as left- or right-handed.  
534 Additionally, experts showed greater dissimilarity between hands and the non-expert  
535 tool (tongs), suggesting that experts have a more distinct representation of general  
536 grasping tools. While we did not have clear hypothesis relating to other sensorimotor  
537 areas more directly involved in motor planning and control, the exploratory analysis  
538 conducted in left parietal cortex provided no evidence supporting a neural embodiment  
539 result. Together, our findings in expert tool users provide contradicting evidence to the  
540 tool embodiment theory.

541

542 There are several potential explanations for the current findings, specifically for how  
543 experience with tools leads to a differentiation between hand and tool representations.  
544 A primary explanation for the present result is the extensive visual tool experience of the  
545 experts. Both short- (Gauthier et al., 1999; Kourtzi et al., 2005; Op de Beeck et al.,  
546 2006; Brants et al., 2016) and long-term (Baker et al., 2007; Chan et al., 2010; McGugin  
547 et al., 2012; Dehaene-Lambertz et al., 2018; Gomez et al., 2019) visual experience  
548 have been shown to shape representations in visual cortex (for review see Op de Beeck  
549 and Baker, 2010; Harel, 2016). For example, visual training with a category of novel  
550 visual objects leads to a differentiation of that category from similar untrained categories

551 (Op de Beeck et al., 2006). Similarly, extensive experience with specific orthographies  
552 leads to a distinct representation of those orthographies compared to other  
553 orthographies (Baker et al., 2007). This is consistent with our recent work demonstrating  
554 that prosthesis usage in amputees leads to greater dissociation of prostheses relative to  
555 hands [and tools (Maimon-Mor and Makin, 2020)].

556

557 Also, while we presume it is the tool representation that has changed in the experts,  
558 perhaps it is the representation of the tool action that has changed. Recent work has  
559 highlighted the role of occipitotemporal cortex in processing observed actions  
560 (Tucciarelli et al., 2019). This would explain why experts show greater dissimilarity  
561 between hands and both their expert tool (litter picker) and a similar grasping tool on  
562 which they did not have prior expertise (tongs). Alternatively, the observed effect for the  
563 non-expert tool relative to hands could potentially be driven simply by the shared visual  
564 features between the expert and non-expert tools. Indeed, previous research has  
565 demonstrated evidence for both of these predictions that OTC encodes information  
566 related to stimuli shape (Chen et al., 2018; Wang et al., 2018), as well as the  
567 functional/semantic properties of the stimuli (Bracci et al., 2015; Chen et al., 2018).

568

569 A second interpretation of the present findings stems from the motor literature which  
570 suggests that perhaps the visual hand representation has changed in the experts.  
571 Multiple studies have shown that the organizational structure of the sensorimotor hand  
572 representation is shaped by the natural statistics of hand usage (Ejaz et al., 2015).  
573 Considering the intrinsic functional connectivity between the visual hand area and the

574 sensorimotor hand representation (Tal et al., 2016) and that the expert tool users  
575 extensively use their hands to interact with tools, perhaps, the representational shift  
576 shown in the experts is driven exclusively by changes in the visual hand representation.  
577 This would also explain why the distances relative to both tools changes.

578

579 A third interpretation is that the mechanism supporting the increased differentiation of  
580 tools from hands observed in experts could be not strictly visual or motor, but rather  
581 driven by a larger cognitive mechanism. For instance, in the memory domain, the  
582 strengthening of representations is associated with pattern separation, thereby making  
583 a new representation less confusable with other memories (Schlichting et al., 2015).  
584 Thus, in the present study, for experts to optimally control a hand or tool, the network  
585 differentiates these representations, to reduce potential interference and most  
586 successfully store and access information.

587

588 It is important to note that our experimental design may have several potential  
589 limitations. First, while viewing first-person videos during fMRI scans engages  
590 visuomotor regions, it did not activate sensorimotor regions (e.g. M1/S1). Considering  
591 sensorimotor cortex is more directly involved in the sensory and motor bodily  
592 experience, the computations within these neural structures could potentially be  
593 different from the pattern observed in occipitotemporal and parietal cortex.  
594 Unfortunately, the fMRI environment poses unique challenges for active experimental  
595 designs involving tool-use, and as highlighted above, the actual sensorimotor  
596 engagement with the tool provides further confounds that we were eager to avoid. Thus,

597 we cannot rule out the possibility that if subjects were actively involved in tool use  
598 during fMRI scans, a different representational structure could have be observed within  
599 these regions. Also, it's possible that while watching the videos, experts are mentally  
600 simulating actions differently to the novices. In this instance, novice behavior could be  
601 more varied in mentally simulating the actions. Previous research is inconclusive on the  
602 engagement of OTC during visual and motor imagery (Orlov et al., 2010; Kikuchi et al.,  
603 2017). It is also challenging, and perhaps counter-productive, to disentangle cognitive  
604 contribution to expert motor learning (Broadbent et al., 2015). Nonetheless, future work  
605 is needed in order to determine whether the motor system produces different  
606 representational solutions to those observed here, to support expert tool use, both  
607 within and beyond the framework of embodiment.

608

609 Finally, it is important to acknowledge the potential limitations of the small sample size  
610 used in the present study. Despite our greatest efforts to recruit more litter-picker  
611 experts (we originally interviewed 52 candidates for the study), we were only able to  
612 secure 7 participants. Small sample sizes are known to lead to an overestimation of the  
613 actual effect size (Button et al., 2013), and a greater uncertainty around the estimate of  
614 the true effect size. Designs with a small sample size are also more susceptible to Type  
615 II errors. Another problem, related to small sample sizes, is that the distribution of the  
616 sample is more likely to deviate from normality, and the limited sample size makes it  
617 often impossible to rigorously test the assumption of normality (Ghasemi and Zahediasl,  
618 2012). While we have attempted to account for some of these issues (e.g. by reporting  
619 the Bayes Factors of the key findings), it is important to place our findings in this limiting

620 context. Where sample size is inherently limited, the advise is to result to replications of  
621 the findings (Makin and Orban de Xivry, 2019). As such, here, we used case-study  
622 statistics to provide independent replications of our key effect, i.e., greater distances  
623 between hands and litter pickers in the experts relative to the novices. Nevertheless,  
624 other evidence presented here, and in particular the exploratory analysis in parietal  
625 cortex, awaits further confirmation.

626

627 In conclusion, while the exact nature for how experience modifies the representational  
628 structure is not yet fully understood, the current study offers a striking proof-of-concept  
629 for the adult human brain's ability for adaptive plasticity, advancing our current  
630 understanding of how categorical selectivity emerges within high level visual cortex. Our  
631 findings provide strong evidence that extensive tool use leads to an increased neural  
632 differentiation between visual representations of hands and tools. This evidence  
633 provides an important alternative framework to the embodiment theory.

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802 **Figure Captions**803 **Table 1. Participant demographics.** Expert litter pickers (EXP).

804

805 **Fig. 1. Neuroimaging hypotheses and experimental paradigm. (A)** An illustration of  
806 the predictions generated by the proposed hypotheses for the neuroimaging  
807 experiment. Under the first, embodiment prediction, extensive tool use could lead to  
808 representations of hands and tools to become neurally integrated, such that tools are  
809 represented more similarly to hands, suggesting that tools are embodied. A second  
810 prediction is that experts will show greater categorization of representations of hands  
811 and tools, such that the neural representations for hands and tools would become  
812 differentiated and more dissimilar to each other. This would suggest that perhaps that  
813 visual experience with tools leads to an increased sharpening of the representation. **(B)**  
814 Examples of the video stimuli shown during the fMRI scan depicting grasping actions  
815 performed by each effector category: hands, litter pickers or tongs (the videos can be  
816 downloaded on the Open Science Framework (OSF) at <https://osf.io/p4q3y/>). To control  
817 for any potential laterality effects, the stimuli included both left and right-handed  
818 versions. **(C)** ROI probability map for all participants (n=19) showing hand and tool  
819 selective OTC, defined using independent functional data. For each participant and  
820 hemisphere, the top 100 most activated voxels of OTC were selected based on a hands  
821 + tools > objects + low level visual stimulus contrast. ROIs from all participants were  
822 superimposed. Warmer colours represent voxels that were included in a greater number  
823 of individual ROIs. Group-specific probability maps of OTC can be downloaded on the  
824 Open Science Framework at <https://osf.io/p4q3y/>.

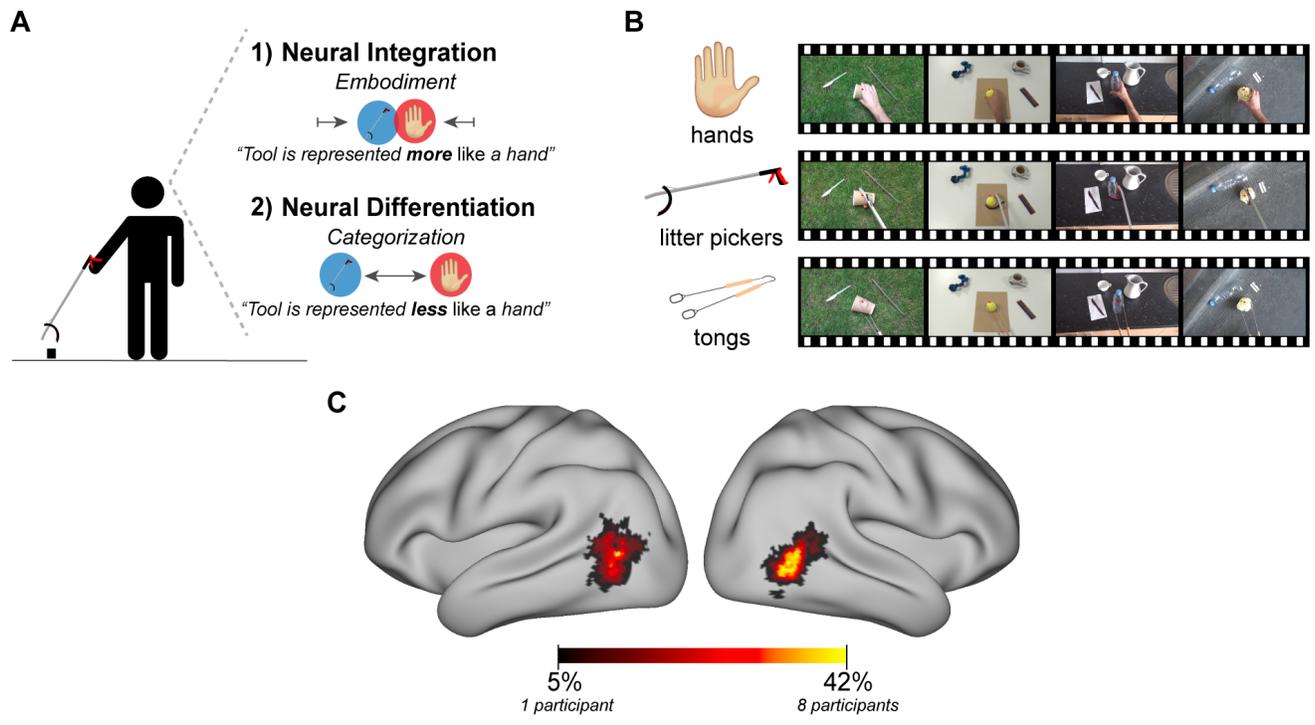
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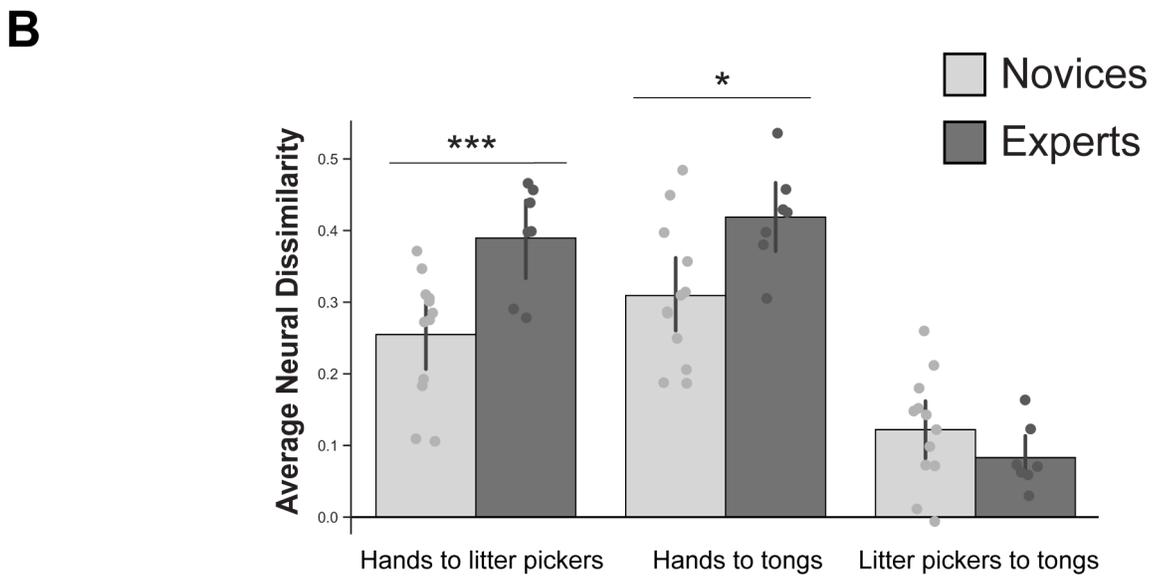
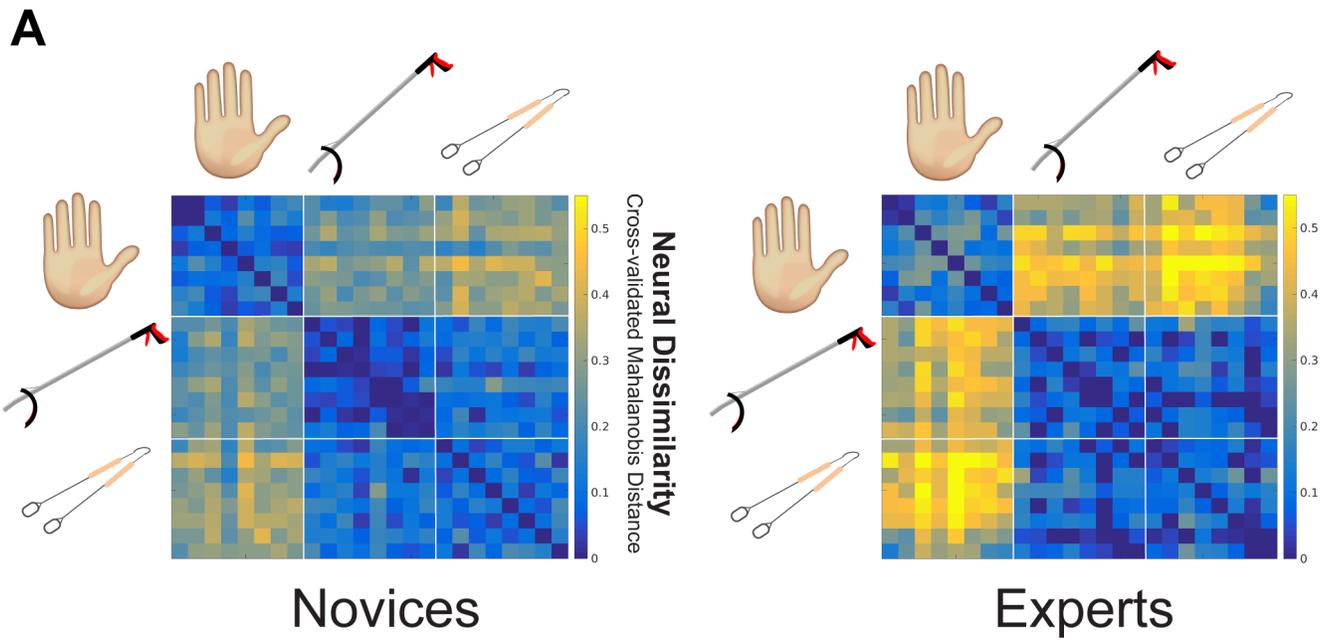
826 **Fig. 2. Expert tool users represent tools less like hands. (A)** Group representational  
827 dissimilarity matrices (RDMs) showing the pairwise distances (cross-validated  
828 mahalanobis distance) between each video condition. Each element in the matrix was  
829 averaged across left and right OTC. Warmer colours indicate the conditions that evoked  
830 more dissimilar patterns of activity. Group multi-dimensional scaling plots derived from  
831 these group RDMs can be accessed at <https://osf.io/p4q3y/>. **(B)** Bar plot of individual

832 participants for each cross-effector category distance pair: hands ↔ litter pickers, hands  
833 ↔ tongs and litter pickers ↔ tongs. These values are generated by averaging the 8x8  
834 pairwise comparison values, for each effector category pair, for each subject  
835 individually. Dark grey values reflect expert tool users (n=7). Light grey values reflect  
836 novices (n=12). Circles depict individual subject means. Values indicate group means ±  
837 standard error. Asterisks denote significance as follows: \* p<0.05; \*\*\* p<0.005.

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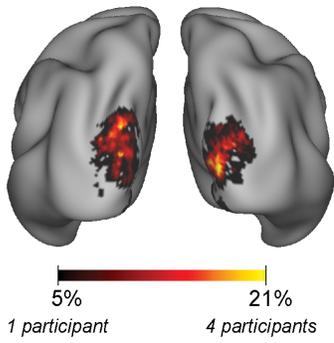
839 **Fig. 3. Analyses in visual cortex and left parietal cortex. (A)** A primary visual cortex  
840 ROI probability map was constructed for all participants (n=19). Warmer colours  
841 represent voxels that were included in a greater number of individual ROIs. **(B)** Group  
842 representational dissimilarity matrices for V1 showing the pairwise distances (cross-  
843 validated mahalanobis distance) between each video condition. Warmer colours  
844 indicate the conditions that evoked more dissimilar patterns of activity. **(C)** A left parietal  
845 cortex ROI probability map for all participants (n=19) showing hand and tool selective  
846 voxels was defined using independent functional data. ROIs from all participants were  
847 superimposed. Warmer colours represent voxels that were included in a greater number  
848 of individual ROIs. **(D)** Group representational dissimilarity matrices for left parietal  
849 cortex showing the pairwise distances (cross-validated mahalanobis distance) between  
850 each video condition. Warmer colours indicate the conditions that evoked more  
851 dissimilar patterns of activity.





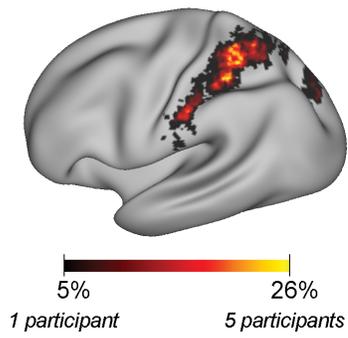
**A**

Visual Cortex

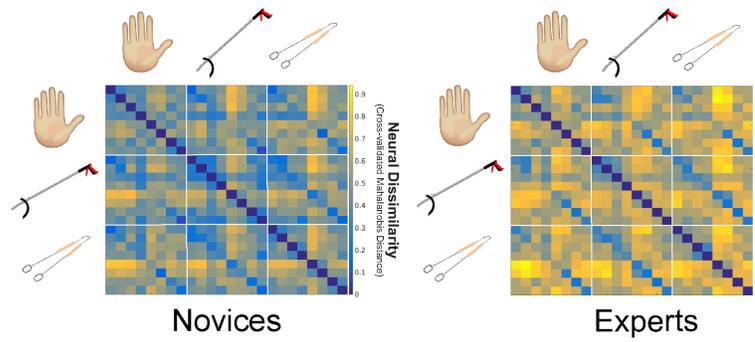


**C**

Left Parietal Cortex



**B**



**D**

