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## Dorsal and ventral stream contribution to the paired-object affordance effect

Alexia Roux-Sibilon, Solène Kalénine, Cédric Pichat, Carole Peyrin

► **To cite this version:**

Alexia Roux-Sibilon, Solène Kalénine, Cédric Pichat, Carole Peyrin. Dorsal and ventral stream contribution to the paired-object affordance effect. *Neuropsychologia*, 2018, 112, p.125 - 134. 10.1016/j.neuropsychologia.2018.03.007 . hal-01741530

**HAL Id: hal-01741530**

**<https://hal.science/hal-01741530>**

Submitted on 22 Nov 2023

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1 **Title:** Dorsal and ventral stream contribution to the paired-object affordance effect

2

3 **Authors:** Alexia Roux-Sibilon<sup>a</sup>, Solène Kalénine<sup>b</sup>, Cédric Pichat<sup>a</sup> & Carole Peyrin<sup>a</sup>

4

5 **Affiliations:**

6 <sup>a</sup> Université Grenoble Alpes, CNRS, LPNC UMR 5105, Grenoble, France

7 <sup>b</sup> Univ. Lille, CNRS, CHU Lille, UMR 9193, SCALab - Sciences Cognitives et Sciences Affectives, F-  
8 59000 Lille, France

9

10 **Corresponding author:**

11 Alexia Roux-Sibilon

12 Laboratoire de Psychologie et NeuroCognition (LPNC)

13 Université Grenoble Alpes

14 BSHM – 1251 Av Centrale CD40700

15 38058 Grenoble Cedex 9

16 France

17 E-mail: [alexia.roux-sibilon1@univ-grenoble-alpes.fr](mailto:alexia.roux-sibilon1@univ-grenoble-alpes.fr)

18

19 **Declarations of interest:** none

20 **Abstract**

21 Visual extinction, a parietal syndrome in which patients exhibit perceptual impairments when two  
22 objects are simultaneously presented in the visual field, is reduced when objects are correctly positioned for  
23 action, indicating that action helps patients' visual attention. Similarly, healthy individuals make faster  
24 action decisions on object pairs that appear in left/right standard co-location for actions in comparison to  
25 object pairs that appear in a mirror location, a phenomenon called the paired-object affordance effect.  
26 However, the neural locus of such effect remains debated and may be related to the activity of ventral or  
27 dorsal brain regions. The present fMRI study aims at determining the neural substrates of the paired-object  
28 affordance effect. Fourteen right-handed participants made decisions about semantically related (i.e.  
29 thematically related and co-manipulated) and unrelated object pairs. Pairs were either positioned in a  
30 standard location for a right-handed action (with the active object – lid – in the right visual hemifield, and  
31 the passive object – pan – in the left visual hemifield), or in the reverse location. Behavioral results showed  
32 a benefit of correctly positioning related pairs for action when performing action decisions (deciding if the  
33 two objects are usually used together), but not when performing contextual decisions (deciding if the two  
34 objects are typically found in the kitchen). Anterior regions of the dorsal stream (e.g. supplementary motor  
35 area) responded to inadequate object co-positioning for action, but only when the perceptual task required  
36 action decisions. In the ventral cortex, the left lateral occipital complex showed increased activation for  
37 objects correctly positioned for action in all conditions except when neither task demands nor object  
38 relatedness was relevant for action. Thus, fMRI results demonstrated a joint contribution of ventral and  
39 dorsal cortical streams to the paired-affordance effect. They further suggest that this contribution may  
40 depend on contextual situations and task demands, in line with flexible views of affordance evocation.

41

42 **Keywords:** visual attention, action, object perception, Lateral Occipital Complex, fMRI

## 43 1. Introduction

44 Human environment is full of objects and objects are most often perceived in subsets of items  
45 grouped along contextual, spatial, and/or functional relationships rather than in isolation. There is now  
46 considerable evidence that the perception of object pairs may be facilitated when objects are correctly  
47 positioned for action (Borghi et al., 2012; Green & Hummel, 2006; McNair & Harris, 2014; Roberts &  
48 Humphreys, 2011; Xu et al., 2015; Yoon et al., 2010). Interest for action-based effects on object perception  
49 has increased after Riddoch, Humphreys and colleagues demonstrated the impact of this factor on  
50 neuropsychological deficits (Riddoch et al., 2002, 2006). Visual extinction is a neuropsychological  
51 syndrome frequently observed after posterior parietal damage, in which patients fail to report the  
52 contralesional stimulus when two stimuli are simultaneously presented in the visual field. Yet extinction  
53 may be reduced when the two object stimuli are correctly positioned for action (e.g., hammer and nail in  
54 adequate orientation for co-action), as demonstrated by an important series of patient studies (Riddoch et  
55 al., 2006). Recovery from visual extinction is not visible for mere associated objects (hammer-mallet), but  
56 has been reported, although to a lower extent, for semantically unrelated objects that could possibly  
57 participate in a common action (bottle-bucket). Neuropsychological findings show that visual attention of  
58 patients with posterior parietal lesions may benefit from action relations between objects. However, the  
59 neural locus of this benefit is not evident and may be related to the relatively preserved functioning of more  
60 dorsal (e.g., superior parietal lobule, anterior parietal sulcus) and/or more ventral (e.g., posterior temporal)  
61 in these patients.

62 Following the thorough description of extinction phenomena, an important series of studies have  
63 further investigated the cognitive and neural mechanisms underlying the facilitation that relevant positioning  
64 for action may provide to the perception of object pairs in healthy participants using different paradigms  
65 (Green & Hummel, 2006; Roberts & Humphreys, 2010; Xu et al., 2015, 2017; Yoon et al., 2010). In one  
66 such study (Yoon et al., 2010), pairs of objects that are typically used together (e.g., frying pan and spatula)  
67 were visually presented from a first-person perspective to right-handed participants. Object relative position  
68 and task were manipulated. Objects could be positioned in a way enabling the co-manipulation of the objects  
69 by right-handers, namely the active object on the right (spatula) and the passive object on the left (frying  
70 pan), or in a mirror position. Participants were asked to perform two judgement tasks. In the action decision  
71 task, they had to decide whether objects would typically be used together whereas in the contextual decision  
72 task they decided whether objects were typically found in the kitchen. A control condition, in which objects  
73 were unrelated (e.g., frying pan and saw), was used for “no” trials. Results highlighted an interaction  
74 between object co-location and task, with a selective advantage of correct co-location for action in the action  
75 decision task: Response times on “yes” trials were faster for correctly co-located objects compared to

76 incorrectly co-located objects when processing the action relation between objects, but not when processing  
77 their spatial context. Results are unlikely due to familiarity of object pairs since the benefit of correct co-  
78 location for action is only visible for this particular type of judgments. The authors attributed the effect to  
79 the “direct route” to action that processes the potential for action between objects bypassing the semantic  
80 system. The direct route to action is assumed to rely on brain regions of the dorsal stream, including the  
81 dorsal premotor and prefrontal cortex (Humphreys et al., 2010) and may thus be involved in processing  
82 affordances for single objects as well as affordances for object pairs. However, as we will review next, the  
83 very few neuroanatomical findings related to the processing of paired-object affordances do not provide any  
84 clear answer to the neural substrate of the effect. Involvement of either dorsal or ventral brain areas has been  
85 alternatively reported with different methodologies and different tasks. The present fMRI study aimed at  
86 clarifying the neural correlates of the paired-object affordance effect.

87         In a recent TMS study, Xu et al. (2017) demonstrated the involvement of certain areas of the dorsal  
88 stream in processing implied actions between objects that are typically used together. Object pairs were  
89 presented in a correct or incorrect co-location for action. The potential for action was manipulated by  
90 changing the orientation of the active object so that it could not interact with the passive object anymore,  
91 rather than by manipulating the congruency between object relative position and participants’ handedness.  
92 In addition, the active object could be positioned on the left or on the right. Participants made left/right  
93 responses to determine the shape of central targets (triangles or circles) that were irrelevant to the objects.  
94 The pattern of behavioral responses in the absence of TMS stimulation (Xu et al., 2015) showed an  
95 advantage for responses aligned with the active object compared to those aligned with the passive object for  
96 correctly co-located objects. Moreover, there was a disadvantage of the responses aligned with the passive  
97 object for correctly co-located objects compared to incorrectly co-located objects. In this paradigm,  
98 activation of affordances for object pairs was reflected by a boost in the salience of the active object when  
99 it was correctly co-located for action. When TMS was applied over the left anterior intraparietal sulcus, the  
100 effect vanished, indicating that regions of the dorsal stream typically associated with affordance perception  
101 in the case of single objects are also involved in the perception of paired-object affordance, even when the  
102 task does not explicitly orient attention towards the action properties of the object. TMS over the lateral  
103 occipital cortex did not affect the effect of implied actions between objects to a similar extent, suggesting a  
104 less critical role of regions of the ventral stream.

105         In contrast, several studies (Kim & Biederman, 2011; Roberts & Humphreys, 2010; but see Baeck  
106 et al., 2013) demonstrated with different experimental paradigms that object co-location for action may be  
107 coded in the lateral occipital complex (LOC). LOC is a key region of the ventral stream for the recognition  
108 of objects (Altmann et al., 2004; Grill-Spector, 2003; Grill-Spector et al., 2001) that is also particularly

109 sensitive to the perception of tools and tool-related actions (see Lingnau & Downing, 2015 for review). In  
110 a fMRI study, Roberts and Humphreys (2010) showed that categorization of objects that are correctly co-  
111 positioned for action (e.g., pitcher in a pouring position above glass) induced greater activation of the LOC  
112 compared to that of objects that are incorrectly positioned for action (e.g., pitcher in a pouring position  
113 below glass). Interestingly, the effect remained present when attention was not directed on the objects  
114 (categorization task performed on different pictures of the display) and when objects were only weakly  
115 semantically related (e.g., pitcher in a pouring position above nail). However, no changes in activation were  
116 found in dorsal brain regions.

117           One way to reconcile the different lines of evidence is to assume that the paired-object affordance  
118 effect may have a double origin. Both dorsal and ventral stream regions may contribute to the coding of  
119 object co-position for action but differently depending on the existing relations between objects and task  
120 demands. In accordance with Kim and Biederman (2011) and Roberts and Humphreys (2010), the LOC  
121 may be sensitive to the correct positioning of objects for action regardless of whether they already share a  
122 strong semantic relationship, and even when the task does not explicitly orient attention to the action  
123 relationship. In contrast, the dorsal involvement in processing action affordances for object pairs may be  
124 more dependent upon stimuli and task context. This is growing evidence showing the activation of motor-  
125 related cerebral areas during object perceptual processing is not as automatic as previously envisaged (see  
126 Van Elk, van Schie, & Bekkering, 2014 for review). For instance, Wamain, Gabrielli and Coello (2015)  
127 reported a stronger recruitment of the motor neural network during visual object processing, as reflected by  
128 enhanced Mu rhythm desynchronization, when the object was presented within reach compared to out of  
129 reach, but only when the task required processing its action-related properties. In another EEG study, Natraj  
130 et al. (2015) found that the additional presence of a hand near during the processing of object pairs increased  
131 early activation of parieto-frontal areas. Using fMRI, Bach et al. (2010) showed that within a large left  
132 frontoparietal network recruited during action observation, the relative involvement of each region  
133 depended on the relation between the tool and the goal object and on the characteristics of the action task.  
134 For instance, maximum activation of the anterior intraparietal sulcus was reported when the task required  
135 to judge whether the relative spatial position of a tool and its recipient (e.g., hole puncher on paper) was  
136 correct (spatiomotor task) compared to when the task required to judge whether the two objects could be  
137 used together to achieve an action goal (functional task). In contrast, greater activation of the middle frontal  
138 gyrus was found during both spatiomotor and functional judgements when tool and goal object shared a  
139 functional relation compared to when objects were not directly used together (e.g., CD and cassette tape).  
140 Together, recent research supports the flexible activation of affordances during the processing of visual  
141 objects, with a greater or lower involvement of motor-related regions of the dorsal stream as a function of  
142 contextual factors and task characteristics.

143           The present study aims at highlighting the flexible contribution of dorsal and ventral stream regions  
144 to the paired-object affordance effect using fMRI. This neuroimaging method allows both whole-brain and  
145 more specific region-of-interest analyses. Thus, the method is best suited to evaluate the possible  
146 involvement of a large fronto-parietal dorsal stream (including the intraparietal sulcus as in Xu et al. 2017,  
147 but also premotor and motor regions) as well as more focal ventral stream regions (e.g., LOC) in coding  
148 affordances for object pairs. The benefit of positioning the two objects in a correct co-location for action  
149 (active object on the right for right-handed participants) was investigated as a function of object relatedness  
150 (tool-recipient versus unrelated objects) and task (action versus contextual decisions). Following Yoon et  
151 al. (2010), but in contrast to Xu et al. (2017), we selected tasks that involve object identification and  
152 manipulated the presence of a semantic relation between objects, two characteristics that are potentially  
153 important to test the recruitment of the ventral stream. However, in contrast to Kim and Biederman (2011)  
154 and Roberts and Humphreys (2010), we considered the relevance of task and stimuli for action by designing  
155 3D realistic object pictures on the one hand, and by directly contrasting action-relevant and action-irrelevant  
156 judgments on the other hand. Context and task demands have both been proved important for affordance  
157 perception for single objects and may be critical for the recruitment of the dorsal stream in the perception  
158 of paired-object affordances.

159           Behaviorally, we expected to find an interaction between object co-location for action, object  
160 relatedness and task. In particular, we predicted a benefit of correctly positioning related objects for action  
161 when the task involved action decisions but not contextual decisions. Furthermore, we predicted the  
162 involvement of both ventral and dorsal stream areas in processing object co-location for action, with ventral  
163 areas being less sensitive to object semantic relatedness and task demands.

164

## 165 **2. Material and methods**

### 166 **2.1. Participants**

167           Fourteen healthy right-handed participants (mean age: 23, 7 women) with normal or corrected-to-  
168 normal vision were included in this study. All participants took part in two experiments: a Paired-Object  
169 Affordance (POA) experiment, which allowed us identifying the functional regions specifically involved in  
170 the paired-object affordance effect, and an independent LOC Localizer experiment, which allowed us  
171 identifying object-selective regions. Participants gave their informed written consent for this study, which  
172 was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of  
173 Helsinki, 2013) and approved by the local ethic committee (CPP ID RCB: 2011-A01551-40).

174

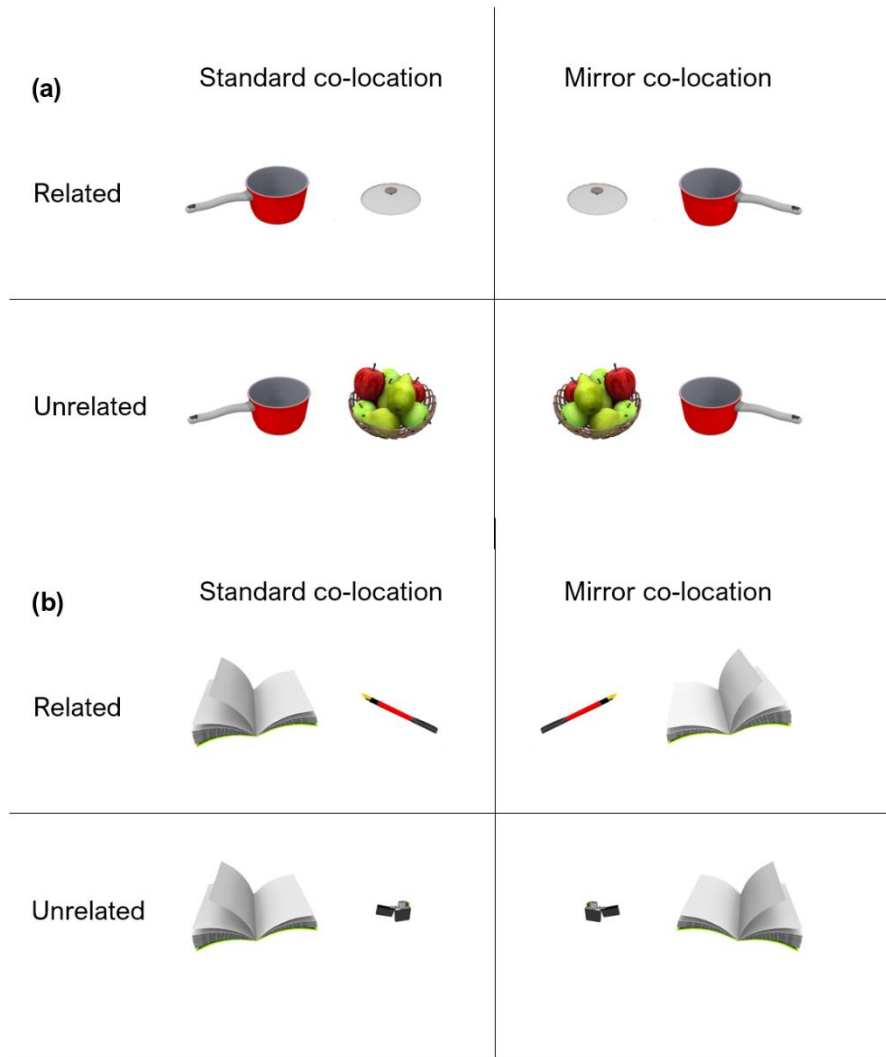
175           2.2. Stimuli and procedure in the POA experiment

176           Stimuli consisted of 3D colored pictures of manipulable artifacts built with Keyshot 5.3.6 software  
177 (Luxion Inc, Tustin, CA, USA). Each object was centered on a white square image, sized to 256 x 256 pixels  
178 (or 6 degrees of visual angle). Angular size of the objects in the square image ranged from 0.6 to 6 degrees  
179 of visual angle. Objects were presented in pairs (Figure 1). One object was presented in the left visual field  
180 and the other was presented in the right visual field following a retinal eccentricity of 3 degrees of visual  
181 angle. The two objects covered in this way a maximal visual field size of 12 degrees of visual angle.

182           Forty object pairs were designed, 20 were pairs of semantically related objects that are thematically  
183 related and co-manipulated (R condition), and 20 were pairs of unrelated objects (UN condition). In the R  
184 condition, each pair was designed in reference to a typical right-handed action. One of the two objects was  
185 a passive object usually held, but not maneuvered, by the left hand (e.g., pan or notebook), and the other  
186 was an active object usually held and manipulated with the right hand (e.g., lid or pen, respectively). In the  
187 UN condition, each pair was made of the same passive object as in the R condition, coupled with another  
188 manipulable artifact unrelated to the passive object. In both R and UN conditions, half of the pairs was  
189 composed of objects typically found in the kitchen (K condition; e.g., pan and lid), and the other half was  
190 composed of objects typically found in another context (NK condition; e.g., notebook and lighter). Finally,  
191 for both R and UN conditions, we manipulated the co-location for action of the two objects. In a first  
192 condition, the passive object – that is the one typically held by the left hand during a right-handed action –  
193 was presented to the left, and the second object – the active or unrelated object – was presented to the right.  
194 Hence, the objects were presented in a standard co-location for a right-handed action (Standard condition).  
195 In a second condition, we applied a symmetrical rotation of the pairs respective to the vertical axis, so that  
196 the presentation of the pair was mirrored relative to the Standard co-location. In this second condition, the  
197 passive object was hence presented on the right and the second object, active or unrelated, was presented on  
198 the left (Mirror condition).

199





200  
 201 **Figure 1.** Examples of stimuli in the POA experiment. Object pairs could be found in the kitchen (a) or not  
 202 (b). In each set, the two objects of a pair were either thematically related and typically co-manipulated (R  
 203 condition) or unrelated (UN condition). Each pair was displayed in Standard (typical right-handed action)  
 204 and Mirror co-locations. In the Standard co-location, the passive object (pan, desk lamp) was positioned on  
 205 the left.

206  
 207 Stimuli were displayed using E-prime software (E-prime Psychology Software Tools Inc.,  
 208 Pittsburgh, USA) and back-projected onto a translucent screen positioned at the rear of the MRI magnet.  
 209 Participants viewed the screen at a distance of about 222 cm via a mirror fixed on the head coil. After being  
 210 installed inside the scanner, participants performed two visual tasks: an “Action Decision” task in which  
 211 they had to decide whether the two objects were typically used together, and a “Contextual Decision” task

212 in which they had to decide whether the two objects were typically found in the kitchen. The order of the  
213 tasks was counterbalanced across participants. Participants responded by pressing the keys of a response  
214 box disposed inside the scanner with their right hand. One of the response key corresponded to the yes  
215 response for the two tasks and the other corresponded to the no response. Half of the participants responded  
216 yes with the forefinger and no with the middle finger, and conversely for the other half. Each trial began  
217 with the presentation of a central black fixation dot on a white screen for 500 ms, followed by the object  
218 pair for 700 ms, and a white screen for 1300 ms, in order to follow an inter-stimuli interval of 2500 ms.  
219 Participants were instructed to fixate the center of the screen (fixation dot) and to answer as quickly and  
220 accurately as possible as soon as the objects appeared on the screen. For each trial, response accuracy and  
221 reaction times (RT, in milliseconds) were recorded. Participants performed a short practice session outside  
222 of the scanner with stimuli that were not subsequently used in the experiment.

223 The experiment included six functional runs, three for the Action Decision task and three for the  
224 Contextual Decision task, following a pseudo-randomized event-related paradigm. Each functional run  
225 lasted 4 min and 25 sec and 106 functional volumes were acquired: 80 test events (20 per experimental  
226 condition) and 26 rest events (with a fixation dot in the middle of the screen, including 6 rest events at the  
227 end of the run). Thus, the experiment included a total of 240 experimental trials (30 trials by experimental  
228 condition: R-K-Standard, R-K-Mirror, R-NK-Standard, R-NK-Mirror, UN-K-Standard, UN-K-Mirror, UN-  
229 NK-Standard, and UN-NK-Mirror; Figure 1). Stimuli displayed during the runs of the Action Decision task  
230 and during those of the Contextual Decision task were strictly identical, only instructions given to the  
231 participant changed according to the visual task. For each task, stimuli were presented according to three  
232 different pseudo-randomized orders, spread across the three functional runs.

233 Preliminary tests were performed in order to assess the strength of the thematic relation and of the  
234 co-action relation in R and UN pairs. For each pair of objects, eighteen participants who did not participate  
235 to the present study judged (1) to what extent the two objects are present in the same context at the same  
236 time, even if they are not directly manipulated with each other (thematic judgment), and (2) to what extent  
237 the two objects are directly manipulated with each other (co-action judgment). Participants rated their  
238 judgements on a 7-point scale from very rarely (level 1) to very frequently (level 7). We calculated mean  
239 rating of each participant for R and UN pairs. We then compared ratings of R and UN pairs. A Wilcoxon  
240 Signed-Ranks Test indicated that R pairs were judged more strongly thematically-related and co-  
241 manipulated than UN pairs (Thematic judgment;  $R = 6.68 \pm 0.40$ ;  $UN = 2.42 \pm 0.86$ ;  $Z = 3.72$ ,  $p < .0001$ ;  
242 Co-action judgment;  $R = 6.78 \pm 0.39$ ;  $UN = 1.36 \pm 0.39$ ;  $Z = 3.72$ ,  $p < .0001$ ).

243

244 2.3. Stimuli and procedure in the LOC Localizer experiment

245 Following the main POA experiment, we performed a separate functional LOC Localizer  
246 experiment in order to localize the functional regions of interest specifically involved in object visual  
247 processing (i.e. the LOC in each hemisphere). The localizer experiment was adapted from previous studies  
248 (Kauffmann et al., 2015; Kourtzi et al., 2003; Musel et al., 2014). Participants viewed grayscale images of  
249 objects and scenes in separate blocks of a block design paradigm. Stimuli were black-and-white (256 gray-  
250 scales) images of objects (manipulable artifacts) and scenes (indoors, beaches, mountains, and cities), all  
251 sized to 256 x 256 pixels (or 6 x 6 degrees of visual angle). We designed two other versions of these images:  
252 a “square-scrambled” version, made by dividing the intact images into 21 x 21 pixels squares and by  
253 randomly spreading them, and a “phase-scrambled” version, made by scrambling the phase of the intact  
254 image in the Fourier domain via random permutation, a procedure allowing to preserve the orientation and  
255 the spatial frequency content of the images but making impossible to extract any semantic content (Goffaux  
256 et al., 2011; Woodhead et al., 2011). The experiment included one functional run. Intact, square-scrambled  
257 and phase-scrambled versions of the scene and object images were presented in distinct blocks. The  
258 functional run lasted 7 min and 20 sec and was composed of 24 15-sec task blocks (four blocks of intact  
259 objects, four blocks of square-scrambled objects, four blocks of phase-scrambled objects, four blocks of  
260 intact scenes, four blocks of square-scrambled scenes, and four blocks of phase-scrambled scenes), each  
261 including 15 same type stimuli, interspersed with eight 10-sec rest blocks with a fixation dot in the center  
262 of the screen displayed against a gray background. Participants performed a ‘one-back’ repetition detection  
263 task. They were instructed to press a button whenever they saw two identical stimuli repeated. This task  
264 guaranteed that participants paid at least as much attention to the square-scrambled and phase-scrambled  
265 stimuli than to the more interesting intact stimuli. Only two repetitions per block were presented. Each  
266 stimulus was presented for 300 ms, with a 600 ms interstimulus interval with a fixation dot in the center of  
267 the screen. The functional run included 176 functional volumes.

268

269 2.4. fMRI acquisition

270 Experiments were performed using a whole-body 3T scanner (Achieva 3.0T TX, Philips, NL) with  
271 a 32-channel head coil at the IRMaGe MRI facility (Grenoble, France). For all functional scans of the two  
272 experiments, the manufacturer-provided gradient-echo/T2\* weighted EPI method was used. Forty-two  
273 adjacent axial slices parallel to the bi-commissural plane were acquired in sequential mode from the bottom  
274 to the top, including the cerebellum. Slice thickness was 3 mm. The in-plane voxel size was 3 x 3 x 3 mm  
275 (240 x 240 x 126 mm field of view acquired with a 80 x 80 pixel data matrix; reconstructed with zero filling

276 to 80 x 80 pixels). The main sequence parameters were: TR = 2.5 s, TE = 30 ms, flip angle = 82°. Before  
277 each functional run, six “dummies scans” were acquired to allow for signal equilibration. Following the  
278 seven functional runs (six for the POA experiment and one for the LOC Localizer experiment), a T1-  
279 weighted high-resolution three-dimensional anatomical volume was acquired, by using a 3D modified  
280 Driven Equilibrium Fourier Transform (MDEFT) sequence (field of view = 256 x 224 x 175; resolution:  
281 1.333 x 1.750 x 1.375 mm; acquisition matrix: 192 x 115 x 128 pixels; reconstruction matrix: 288 x 288 x  
282 128 pixels).

283

## 284 2.5. Data analysis

285 Behavioral data (accuracy and response times) were analyzed using STATISTICA 10.0 software.  
286 FMRI data were analyzed with SPM12 (SPM, Wellcome Department of Imaging Neuroscience, London,  
287 U.K.) implemented in MATLAB (Mathworks Inc., Sherbon, MA, USA). Functional volumes were  
288 realigned to correct for head movements to the mean functional image using a rigid body transformation,  
289 time-corrected, normalized into the MNI space and spatially smoothed by an 8-mm FWHM (Full Width at  
290 Half Maximum) Gaussian kernel. Time-series for each voxel were high-pass filtered (1/128 Hz cutoff) to  
291 remove low-frequency noise and signal drift.

292 For the main POA experiment, fMRI signal was analyzed using the general linear model (Friston  
293 et al., 1995) for event-related design. For each participant, 16 conditions of interest (R-K-Standard, R-K-  
294 Mirror, R-NK-Standard, R-NK-Mirror, UN-K-Standard, UN-K-Mirror, UN-NK-Standard, UN-NK-Mirror  
295 for the Action Decision and Contextual Decision tasks) were modeled as 16 regressors convolved with a  
296 canonical hemodynamic response function (HRF). For each event, the amplitude of the HRF was adjusted  
297 by a parametric modulation based on the response time value of the participant for the corresponding  
298 experimental trial. This approach considers the relation between hemodynamic activity and response time,  
299 and hence allows to consider the BOLD activity linked to the conditions of interest regardless of the BOLD  
300 activity linked to the response execution time. Movement parameters derived from realignment corrections  
301 (three translations and three rotations) were also modeled into the design matrix as additional factors of no  
302 interest to account for head motion-related variance. Analyses were performed at the individual subject level  
303 to examine the different contrasts of interest between estimated parameters of the different experimental  
304 conditions. These contrast images were then entered into second-level random effect analyses to test for  
305 within group effects (one-sample t tests). The significance of activations was assessed with a statistical  
306 threshold of  $p < .001$ , uncorrected for multiple comparisons, with a minimum cluster extent of 10 voxels.

307 For the LOC Localizer experiment, fMRI signal was analyzed using the general linear model for  
308 block design. For each participant, the six experimental conditions (intact, square-scrambled, and phase-  
309 scrambled versions of scenes and objects) and rest were modeled as seven regressors, constructed as box-  
310 car functions convolved with a canonical HRF. Movement parameters derived from realignment corrections  
311 (three translations and three rotations) were also modeled into the design matrix as additional factors of no  
312 interest. The LOC was identified in each hemisphere for each participant using the [intact objects > intact  
313 scenes], [intact objects > square-scrambled objects], and [intact objects > phase-scrambled objects]  
314 contrasts. The significance of activations was assessed with a statistical threshold of  $p < .05$  uncorrected.  
315 For certain participants, significant clusters extended on the whole inferior occipito-temporal cortex. Thus,  
316 small sphere ROIs (3-mm radius) were created in each hemisphere, centered at the peak of activation in the  
317 posterior part of the inferior occipito-temporal cortex, close to the peak activations reported by Roberts and  
318 Humphreys (2010), i.e. MNI y coordinate = -68 mm in the left hemisphere and -65 mm in the right  
319 hemisphere. These sphere LOC ROIs served as the structural constraint for the analysis of the data in the  
320 main POA experiment. Parameter estimates (% signal change relative to the global mean intensity of signal)  
321 of event-related responses were extracted from the two LOC ROIs for each participant.

322

### 323 3. Results

#### 324 3.1. Behavioral results

##### 325 3.1.1. Mean error rates (mER)

326 Global mER was very low ( $7.22 \pm 0.59\%$ ), indicating that the tasks were easy to perform. The  
327 Shapiro-Wilk normality test suggests that the mER were not normally distributed for most of the  
328 experimental conditions. Therefore, and because of the low global mER, mER were examined by the mean  
329 of a non-parametric test (independence Khi2). The main objective of this study was to assess the impact of  
330 object co-location for action as a function of the relationship between objects and task demands (action vs.  
331 contextual decisions). Thus, we tested the difference in mER between the Standard and Mirror conditions  
332 for the R and UN pairs in each task.

333 For R pairs, results did not show significant difference between Standard and Mirror conditions  
334 neither in the Action decision task ( $\chi^2(1, N = 14) = 3.05, p = .08$ ) nor in the Contextual Decision task ( $\chi^2$   
335  $(1, N = 14) = 0.74, p = .39$ ). Similarly, for UN pairs, there was no difference between Standard and Mirror  
336 conditions neither in the Action decision task ( $\chi^2(1, N = 14) = 0.95, p = .32$ ) nor in the Contextual Decision  
337 task ( $\chi^2(1, N = 14) = 1.24, p = .27$ ).

338

339 *3.1.2. Mean correct responses times (mRT)*

340 The Shapiro-Wilk normality test suggested that mRT were normally distributed for all experimental  
341 conditions. A 2×2×2 repeated-measure ANOVA was conducted on mRT with Task (Action Decision and  
342 Contextual Decision), Semantic relation (R and UN), Co-location for action (Standard and Mirror), and  
343 Category (K and NK) as within-subject factors. Mean comparisons were explored using planned  
344 comparisons and effect sizes were estimated by calculating the partial eta-squared ( $\eta^2$ ). Significance level  
345 was fixed at  $p < 0.05$ .

346 The ANOVA conducted on mRT showed main effects of Task ( $F(1,13) = 36.99, p < .001, \eta^2 = .74$ ),  
347 of Semantic relation ( $F(1,13) = 54.50, p < .001, \eta^2 = .81$ ), and of Co-location for action ( $F(1,13) = 43.18, p$   
348  $< .001, \eta^2 = .77$ ). Participants were faster for Contextual Decision ( $630 \pm 23$  ms) than Action Decision ( $729$   
349  $\pm 32$  ms), for R pairs ( $646 \pm 25$  ms) than for UN pairs ( $711 \pm 30$  ms) and when objects were presented in  
350 mirrored ( $668 \pm 27$  ms) compared to standard co-location ( $691 \pm 28$  ms).

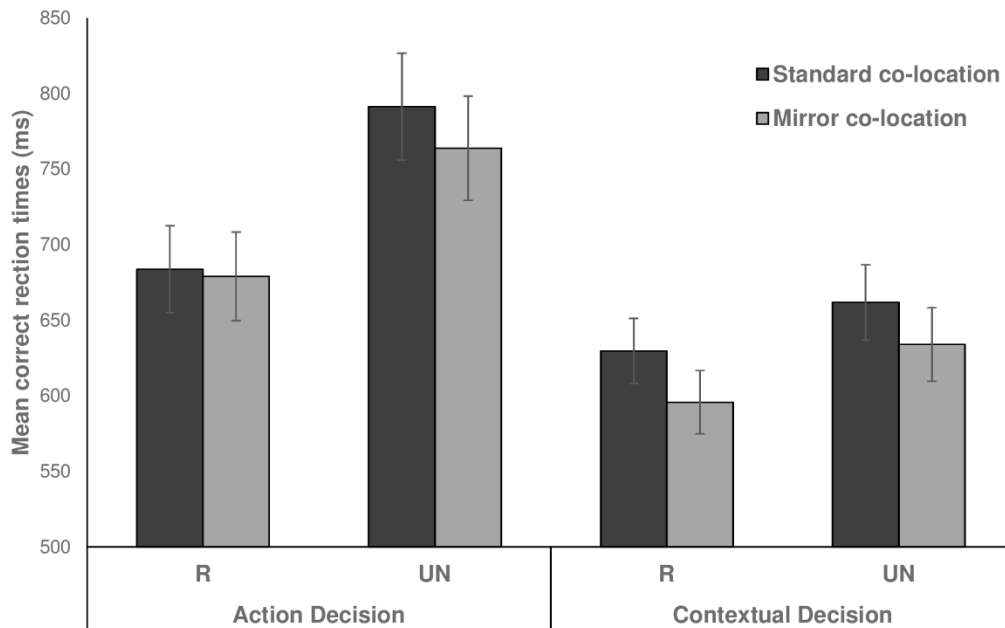
351 In addition, there was a significant interaction between Task and Semantic relation ( $F(1,13) = 62.37,$   
352  $p < .001, \eta^2 = .83$ ). Planned comparisons revealed that responses for R pairs were faster than those for UN  
353 pairs in both the Action Decision task ( $F(1,13) = 67.87, p < .001$ ) and the Contextual Decision task ( $F(1,13)$   
354  $= 23.92, p < .001$ ). Importantly, the difference between R and UN pairs was greater in the Action Decision  
355 task (R:  $681 \pm 29$  ms; UN:  $777 \pm 35$  ms) than in the Contextual Decision task (R:  $612 \pm 21$  ms; UN:  $645 \pm$   
356  $24$  ms).

357 There was no significant interaction between Semantic relation and Co-location for action ( $F(1,13)$   
358  $= 3.50, p = .08$ ), but these two factors interacted with Task ( $F(1,13) = 6.30, p < .05, \eta^2 = .33$ ; Figure 2). In  
359 the Contextual Decision task, participants were slower when objects were presented in standard than mirror  
360 co-location for both UN pairs ( $F(1,13) = 24.06, p < .001$ ; Standard:  $662 \pm 25$  ms, Mirror:  $634 \pm 24$  ms) and  
361 R pairs ( $F(1,13) = 16.74, p < .05$ ; Standard:  $630 \pm 22$  ms, Mirror:  $596 \pm 21$  ms). In the Action Decision task,  
362 participants were slower when objects were presented in standard than mirror co-location for UN pairs  
363 ( $F(1,13) = 14.62, p < .05$ ; Standard:  $791 \pm 35$  ms, Mirror:  $764 \pm 34$  ms), but not for R pairs ( $F(1,13) < 1$ ;  
364 Standard:  $791 \pm 35$  ms, Mirrored:  $764 \pm 34$  ms). Finally, there was no significant main effect or interaction  
365 involving Category (all  $F(1,13) < 1$ )

366 Behavioral results indicated that the advantage of related pairs over unrelated pairs is greater for  
367 action decisions than contextual decisions. In addition, the critical pattern of interaction between object co-  
368 location for action, object relatedness and task was found. Results highlighted a benefit of correctly  
369 positioning pairs of related objects when participants performed action decisions but not contextual

370 decisions. Overall, decisions were slower when the active object was positioned on the right (correct co-  
371 location) than on the left. Yet this general cost disappeared when participants identified that related objects  
372 could be typically used together. This suggests that action decisions enhanced the salience of motor  
373 information, and thus facilitated the processing of semantic relations between objects that are correctly  
374 positioned for action.

375



376  
377 **Figure 2.** Mean correct reaction times (milliseconds) as a function of Task (Action Decision vs. Contextual  
378 Decision), the semantic relation (Related: R vs Unrelated: UN) and Co-location of objects (Standard vs.  
379 Mirror). Errors bars correspond to standard errors.

380

### 381 3.2. fMRI results

#### 382 3.2.1. Whole brain analysis

383 Since statistical analysis of mER and mRT revealed no effect of category (kitchen versus non  
384 kitchen), this factor has not been further considered in the analysis of fMRI data. First, we examined the  
385 effect of Task by contrasting activations elicited by Action Decision and Contextual Decision (Table 1).  
386 The Action Decision task ([Action > Contextual] contrast) recruited a medial frontal region extending from  
387 the anterior cingulate gyrus (BA 32) to the supplementary motor area (BA 6). The Contextual Decision task

388 ([Contextual > Action] contrast) recruited the right middle frontal gyrus (BA 8), as well as the left inferior  
 389 parietal lobule (IPL, BA 40).

390 Then, we examined the effect of Semantic relation. The R pairs ([R > UN] contrast activated the  
 391 superior temporal gyrus (BA 22) bilaterally. In the left hemisphere, the cluster of activation laid between  
 392 the superior temporal gyrus and the inferior parietal lobule (IPL, BA 40), within the temporo-parietal  
 393 junction. The right superior parietal lobule (SPL, BA 7) and the anterior cingulate gyrus (BA 32) were also  
 394 activated. The UN pairs ([UN > R] contrast) activated the LOC.

395  
 396 **Table 1.** Cerebral regions specifically activated for (a) the effect of Task, (b) the effect of Semantic relation,  
 397 and (c) the effect of object Co-location for each Task and Semantic relation. MNI coordinates (x, y, z) of  
 398 the peak are indicated. Activations are reported at a statistical threshold of  $p < .001$ , uncorrected for multiple  
 399 comparisons, and a minimum cluster extent of 10 voxels, except \* $k = 4$ . R = right hemisphere; L = left  
 400 hemisphere; BA = Brodmann's area.

	Side	BA	k	x	y	z	t
<b>(a) Effect of Task</b>							
<b>[Action Decision &gt; Contextual Decision]</b>							
Anterior cingulate gyrus/Supplementary motor area	L/R	32/6	15	9	17	44	4.88
<b>[Contextual Decision &gt; Action Decision]</b>							
Middle frontal gyrus	R	8	24	33	29	47	5.29
Inferior parietal lobule	L	40	20	-51	-55	41	4.56
<b>(b) Effect of Semantic relation</b>							
<b>[Related &gt; Unrelated]</b>							
Superior temporal gyrus/Inferior parietal lobule	L	22/40	38	-60	-43	20	6.74
Superior temporal gyrus	R	22	42	57	-28	14	6.24
	R	38	38	48	2	-10	4.77
Anterior cingulate gyrus	L	32	22	-9	38	5	5.59
Postcentral gyrus	R	5	16	36	-43	65	4.83
<b>[Unrelated &gt; Related]</b>							
Lingual gyrus/Fusiform gyrus (LOC)	R	18/19 /37	828	30	-76	-10	10.86
Lingual gyrus/Fusiform gyrus (LOC)	L	18/19 /37	404	-27	-49	-13	8.00
Medial frontal gyrus (Supplementary motor area)	L/R	6	302	12	11	50	7.35
Inferior frontal gyrus	R	45	28	39	23	8	6.72
Middle frontal gyrus	R	46	76	54	29	29	6.10
	L	46	31	-45	35	17	5.01
<b>(c) Effect of Co-location depending of Task and Semantic relation</b>							
<b>Action Decision task</b>							
<b>- Related object pairs</b>							
<b>[Standard &gt; Mirror]</b>							
Inferior occipital gyrus/Fusiform gyrus (LOC)	L	19	4*	-42	-67	-16	4.79
<b>[Mirror &gt; Standard]</b>							
Medial frontal gyrus (Supplementary motor area)	L/R	6	32	-3	20	59	6.45
	L/R	9	36	3	47	32	4.05
Middle temporal gyrus	R	21	21	33	-4	-16	7.41
	L	21	15	-45	-4	-22	5.34



Cuneus	L	17	19	-18	-100	5	6.07
Posterior cingulate gyrus	L	31	16	-15	-40	38	4.98
<b>- Unrelated object pairs</b>							
<b>[Standard &gt; Mirror]</b>							
Inferior occipital gyrus/Inferior temporal gyrus (LOC)	L	19/37	57	-36	-70	-4	6.64
<b>[Mirror &gt; Standard]</b>							
<i>No significant cluster</i>							
<b>Contextual decision task</b>							
<b>- Related object pairs</b>							
<b>[Standard &gt; Mirror]</b>							
Middle occipital gyrus/Inferior temporal gyrus (LOC)	L	19/37	11	-45	-52	-13	4.92
			10	-48	-64	-7	4.38
<b>[Mirror &gt; Standard]</b>							
<i>No significant cluster</i>							
<b>- Unrelated object pairs</b>							
<b>[Standard &gt; Mirror]</b>							
Inferior frontal gyrus	L	45	23	-51	35	8	6.22
<b>[Mirror &gt; Standard]</b>							
Cuneus	R	17	53	18	-85	-1	5.85
	R	18/19	14	18	-91	23	5.26
	L	18	10	-21	-91	14	4.80

401

402 Following our hypothesis, we examined the effect of Co-location for action of R and UN pairs in

403 each task (Table 1 and Figure 3). For R pairs in the Contextual Decision task, the standard co-location of

404 objects ([Standard > Mirror] contrast) activated the left LOC (BA 19/37), and no significant activation was

405 observed for a mirror co-location of objects ([Mirror > Standard] contrast). For R pairs in the Action

406 Decision task, the standard co-location of objects also activated the left LOC. However this time, the mirror

407 co-location of objects activated several regions of the dorsal stream (supplementary motor area, SMA, BA

408 6; bilateral medial frontal gyrus, BA 9), the bilateral middle temporal gyrus (BA 21) extending in the right

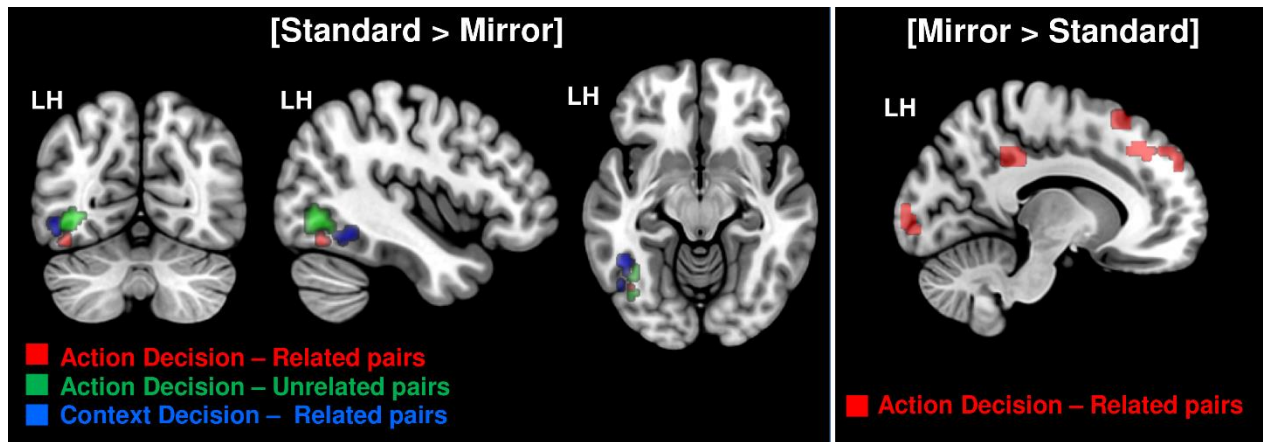
409 parahippocampal gyrus, the left cuneus (BA 17), and the left posterior cingulate gyrus (BA 31). For UN

410 pairs in the Contextual Decision task, the standard co-location activated the left inferior frontal gyrus (BA

411 45), and the mirror co-location activated the cuneus bilaterally (BA 17/18/19). For UN pairs in the Action

412 Decision task, once again the standard co-location activated the left LOC, and no significant activation was

413 observed for the mirror co-location.



415  
 416 **Figure 3.** Effect of object co-location on cerebral activations revealed by [Standard > Mirror] and [Mirror  
 417 > Standard] contrasts depending on the semantic relation between objects (Related vs. Unrelated) and the  
 418 task (Action Decision vs. Contextual Decision). LH: left hemisphere.

419

### 420 3.2.2. ROIs analysis

421 The LOC ROIs were defined in each participant based on the independent Localizer experiment,  
 422 and were used as the structural constraint for the analysis of the data in the POA experiment. The LOC was  
 423 identified in each hemisphere and in each participant based on the [intact objects > phase-scramble objects]  
 424 contrast. In each identified region, the activation peaks that best correspond to previous results in the  
 425 literature (Grill-Spector et al., 2001; Altmann et al., 2004; Roberts & Humphreys, 2010) were selected to  
 426 create two spherical ROIs independently for each participant (see Figure 4): the left LOC (mean MNI  
 427 coordinates and standard deviations:  $x = -39 \pm 5$ ,  $y = -78 \pm 6$ ,  $z = -9 \pm 7$ ) and the right LOC ( $x = 39 \pm 3$ ,  $y =$   
 428  $-78 \pm 5$ ,  $z = -8 \pm 5$ ). Parameters estimates (% signal change relative to the global mean intensity of signal)  
 429 were extracted from the two sphere ROIs for each participant. The average parameter of activity was then  
 430 calculated for each experimental condition. These values were submitted to a repeated measures ANOVA  
 431 for each ROI with Task (Action Decision and Contextual Decision), Semantic relation (R and UN), and Co-  
 432 location for action (Standard and Mirror) as within-subject factors.

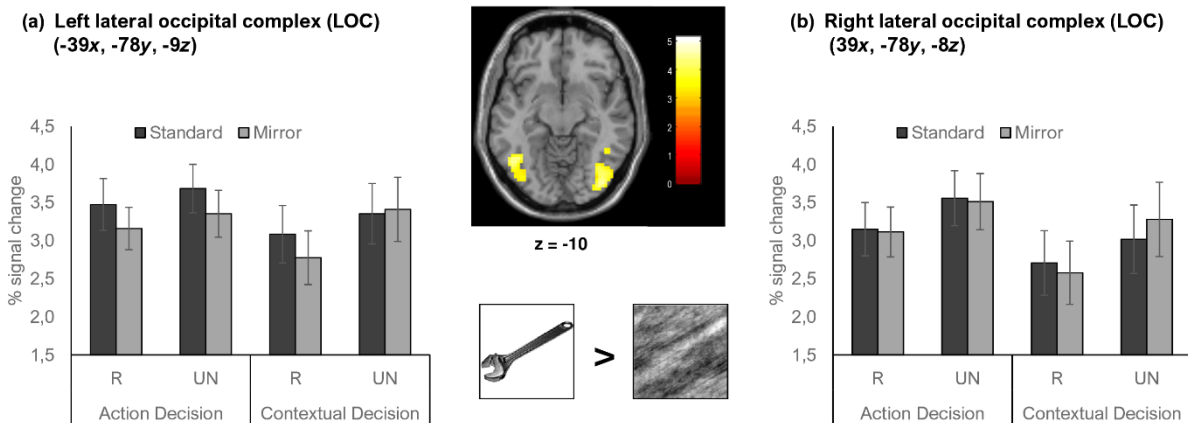
433 For the left LOC, there was a main effect of Semantic relation. UN pairs elicited more activation  
 434 than R pairs ( $F(1,13) = 11.15$ ,  $p < .05$ ,  $\eta^2 = .46$ ). The main effect of object co-location was also significant.  
 435 The left LOC was more activated when the two objects were in standard co-location than in mirror co-  
 436 location ( $F(1,13) = 10.54$ ,  $p < .05$ ,  $\eta^2 = .45$ ). Semantic relation did not interact with Co-location ( $F(1,13) =$   
 437  $1.62$ ,  $p = .22$ ), but these variables interacted with Task ( $F(1,13) = 4.80$ ,  $p < .05$ ,  $\eta^2 = .27$ ). For R pairs, the  
 438 Standard co-location of objects elicited more activation than the Mirror co-location both in the Action

439 Decision task ( $F(1,13) = 6.34, p < .05$ ) and in the Contextual Decision task ( $F(1,13) = 13.94, p < .05$ ). For  
 440 UN pairs, the Standard co-location of objects elicited more activation than the Mirror co-location in the  
 441 Action Decision task ( $F(1,13) = 7.17, p < .05$ ), but not in the Contextual Decision task ( $F(1,13) < 1$ ).

442 For the right LOC, there was also a main effect of Semantic relation ( $F(1,13) = 29.00, p < .001, \eta^2$   
 443  $= .69$ ). UN pairs elicited more activation than R pairs. The main effect of Task was also significant ( $F(1,13)$   
 444  $= 5.33, p < .05, \eta^2 = .30$ ). The right LOC was more activated in the Action decision task than in the  
 445 Contextual decision task. However, the main effect of object co-location was not significant ( $F(1,13) < 1$ ).  
 446 Interactions did not reach significance in the right LOC, neither between Semantic relation and co-location  
 447 of objects ( $F(1,13) = 3.63, p = .08$ ), nor between Task, Semantic relation, and co-location of objects ( $F(1,13)$   
 448  $= 3.14, p = .10$ ).

449 To summarize, ROIs analyses indicated that the left and right LOCs were sensitive to different  
 450 sources of action-related information when processing object pairs, beyond the mere presence of a semantic  
 451 relation between objects. While right LOC was sensitive to the relevance for action of the perceptual task,  
 452 left LOC importantly responded to object co-location for action. Critically, the interaction between Semantic  
 453 relation, Task, and object co-location in the left LOC reflected a greater activation of this region for Standard  
 454 co-locations in all conditions except for the UN pairs in the Contextual Decision task, that is when neither  
 455 the task nor the relationship between objects orient perceptual processing towards action relevant  
 456 information.

457



458

459 **Figure 4:** Bilateral activation of the Lateral Occipital Complex (LOC) during the perception of object pairs  
 460 illustrated on a representative participant. The LOC ROIs were defined independently for each participant  
 461 by contrasting intact objects to phase-scrambled objects: [Intact Objects > Phase-Scrambled Objects].

462 Parameters estimates were then extracted from ROIs for each participant and each experimental condition:  
463 Task (Action Decision vs. Contextual Decision), Semantic relation (Related-R vs. Unrelated-UN), and  
464 object Co-location (Standard vs. Mirror). Graphs represent the mean percentage of signal change for each  
465 ROI. Error bars correspond to standard errors.

466

#### 467 **4. Discussion**

468 This fMRI study aimed to investigate the involvement of dorsal and ventral brain streams in the  
469 paired-object affordance effect. Right-handed participants performed action versus contextual judgments on  
470 object pairs that could be thematically related and co-manipulated or unrelated on the one hand, and  
471 positioned in a correct co-location for action (active object on the right for right-handed participants) or in  
472 the reverse co-location on the other hand.

473 Behavioral results indicated that, similarly to Yoon et al. (2010), the advantage of related pairs over  
474 unrelated pairs was more pronounced when the task demanded action judgments (i.e. determine if the two  
475 objects are typically used together) compared to when the task required contextual judgements. At first  
476 sight, the interaction between object relatedness and task supports previous findings suggesting a close  
477 connection between thematic knowledge and action knowledge (Kalénine & Buxbaum, 2016; Pluciennicka  
478 et al., 2015; Tsagkaridis et al., 2014). A non-alternative interpretation may be related to the extent to which  
479 object pairs afford common actions. Affordances may still be perceived between unrelated objects that may  
480 be used together in certain circumstances, even if it is not typically the case (see for example Chrysikou &  
481 Thompson-schill, 2011; Glenberg & Robertson, 2000 for work on creative object use and novel  
482 affordances). Although object pairs were not rated on this dimension, it is likely that unrelated objects pairs  
483 are also perceived as less compatible with using objects together, in addition to (or rather than) being  
484 semantically unrelated. This may explain why unrelated objects are particularly difficult to process in the  
485 action judgement task.

486 Regarding the effect of co-location for action, results first showed a processing cost of the standard  
487 co-location for related pairs in the particular case of contextual decisions. One possibility is that the  
488 presentation of closely related objects entails automatic processing of paired object affordances, drawing  
489 visual attention on object properties that are not fully relevant for the current task, namely determining  
490 whether the two objects are typically found in the kitchen. Such a processing cost was not reported by Yoon  
491 et al. (2010). They found no statistical difference between standard and mirror co-locations of related objects  
492 in the Contextual decision task, but RTs were descriptively longer for standard co-locations. In the present  
493 study, a similar processing cost was also observed for unrelated pairs in both tasks. Although this cost was

494 rather unexpected, the direction of the effect of object co-location for unrelated pairs was difficult to predict  
495 a priori. In Yoon et al. (2010), unrelated object pairs (“no” responses) were analyzed separately and were  
496 not sensitive to the effect of object co-location for action. The reason why participants were slower to  
497 process unrelated object pairs presented in standard co-location in our study remains unclear. One possible  
498 interpretation is related to individual objects properties. Many passive objects of our stimuli base (e.g., pan,  
499 cup, glass, bottle, etc.) may individually elicit stronger motor affordances than unrelated objects (e.g.,  
500 ashtray, vessel, bin, alarm clock, etc.) especially when positioned on the right, matching a right hand holding  
501 the object as in the mirror co-location condition. Passive objects of unrelated pairs could thus have been  
502 mostly treated individually rather than as in a pair, disrupting the two tasks based on the processing of both  
503 objects.

504 Critically, the processing cost of standard co-location was not found for related pairs in the action  
505 decision task, suggesting that, in line with our hypotheses, an action-relevant task enhanced the salience of  
506 motor information, thus allowing a better processing of action relations between objects when they are  
507 correctly positioned for action. Processing of paired-object affordances appeared context- and task-  
508 sensitive, as both the presence of a semantic relation between objects and the relevance of the task for action  
509 influenced the effect of correctly positioning object for action. Thus, our study provides behavioral  
510 arguments in favor of a flexible processing of paired-object affordances.

511 Although the general neural substrates of thematic relations was not the focus of the present study  
512 and the comparison between related and unrelated pairs was possibly contaminated by task demands, we  
513 verified that processing of thematically-related objects involved the cortical network previously reported in  
514 the literature. This network includes the temporo-parietal junction, the IPL, and the posterior part of the  
515 middle and superior temporal gyri, mainly in the left hemisphere (de Zubicaray et al., 2013; Kalénine et al.,  
516 2009; Kalénine & Buxbaum, 2016; Sass et al., 2009; Schwartz et al., 2011; Tsagkaridis et al., 2014). The  
517 related vs. unrelated contrast indeed revealed a cluster of activation in the posterior part of the left temporo-  
518 parietal cortex. Furthermore, when we examined the cortical regions differently involved in the two  
519 judgment tasks, results showed that contextual judgments, compared to action judgments, recruited the left  
520 IPL. Considering that contextual decisions required the explicit search of thematic connections between  
521 objects in relation to the kitchen context, the left IPL may be specifically involved in this process, regardless  
522 of whether a thematic relation is actually present or not (related and unrelated pairs). These results thus  
523 provide additional evidence for an important role of the posterior parieto-temporal cortex in the processing  
524 of thematic relations.

525 Action judgements compared to contextual judgments activated the supplementary motor area  
526 (SMA), a brain region typically involved in action processing and found to play a crucial role in bimanual

527 movement coordination (Sadato et al., 1997; Serrien et al., 2002). In addition, a recent fMRI meta-analysis  
528 on over 60 research articles (Héту et al., 2013) reported a constant activation of the SMA, among other  
529 frontal regions (e.g., middle and inferior frontal gyrus), for tasks involving motor imagery. These frontal  
530 regions were found in particular for upper limbs motor imagery and for objects-directed actions. Therefore,  
531 it is likely that action decisions (i.e. deciding if the two objects are typically used together) involve motor  
532 imagery strategies recruiting medial frontal regions like the SMA.

533         Considering the main objective of our study, we aimed at determining the respective role of ventral  
534 (LOC) and dorsal cortical streams in coding of object co-location for action. We found evidence both for  
535 dorsal and ventral involvement. First, results showed a medial frontal activation corresponding to the  
536 supplementary motor area (SMA) when the two objects of a related pair were incorrectly co-located for  
537 action ([Mirror>Standard] contrast). Importantly, this pattern was observed only when action judgments,  
538 but not contextual judgments, were made. Following an interpretation based on motor imagery and/or motor  
539 simulation, BOLD response in the SMA would thus increase during performance of action judgements when  
540 participants simulate a more ‘difficult’ action, that is when the two objects are presented in an unusual co-  
541 location for a right-handed action (compared to a more fluent standard co-location). This pattern is  
542 consistent with the contribution of the dorsal stream to the paired-object affordance effect, as suggested by  
543 previous behavioral findings (Green & Hummel, 2006; Yoon et al., 2010; Riddoch et al., 2003, 2006; Xu et  
544 al., 2015) and highlighted in the recent TMS study of Xu et al. (2017). While Xu et al. (2017) demonstrated  
545 a critical role of the posterior part of the dorsal stream in in processing object pairs correctly co-located for  
546 joint action, we first showed activations of anterior motor regions of the dorsal stream such as SMA,  
547 premotor cortex and primary motor cortex in relation to paired-object affordance perception. In Xu et al.  
548 (2017), participants had to make left/right responses to determine the shape of foveally presented targets  
549 (triangles or circles), while pairs of objects correctly or incorrectly co-located for action were seen  
550 parafoveally. Object pairs were thus irrelevant to the task, but nevertheless induced a facilitation of the  
551 categorization task when the active object was aligned with the hand giving the response, that vanished  
552 when TMS stimulation was applied on the left anterior intraparietal sulcus. Using tasks that required explicit  
553 object processing, we did not find any involvement of parietal areas in processing co-location of objects for  
554 action. Instead, explicit processing of action relations between objects (action decision task) recruited the  
555 SMA. It is thus possible that the explicit vs. implicit processing of object pairs determines the relative  
556 involvement of anterior vs. posterior regions of the dorsal stream in coding object co-location for action,  
557 with the SMA selectively contributing to explicit action judgments through motor imagery. Premotor and  
558 frontal regions activations have been observed in several neuroimaging studies on single object affordance  
559 (Chao & Martin, 2000; Grèzes & Decety, 2002). In a fMRI study investigating the neural correlates of  
560 graspable object representations, Creem-Regehr & Lee (2005) showed SMA activation when participants

561 were imagining grasping objects, either real tools (e.g., a brush) or non-object 3D shapes, suggesting that  
562 SMA involvement is independent of object semantics. Our results suggest that SMA may not only contribute  
563 to the processing of single object affordances, but also of paired-object affordances, in addition to be directly  
564 involved in effective bimanual manipulation of object pairs. Future research should investigate whether  
565 disrupting SMA affects the effect of object co-location for action during object processing.

566         The selective contribution of the dorsal stream to the explicit processing of paired-object  
567 affordances when objects are presented in a difficult position for their use is consistent with the hypothesis  
568 of a joint but flexible involvement of dorsal and ventral brain areas in affordance processing (Binkovski &  
569 Buxbaum, 2015; Buxbaum & Kalénine, 2010; Kalénine & Buxbaum, 2015; Rizzolatti & Matelli, 2003).  
570 The potential for co-action of related objects is largely dependent upon object semantics (i.e. object typical  
571 use), which involves the ventral stream processing. Therefore, the recruitment of the dorsal stream during  
572 the identification of familiar thematic relations between objects is probably minimal in regular  
573 circumstances (e.g. standard co-location). Yet the identification of the same familiar relations when objects  
574 are not in a regular position would require additional online spatiomotor transformations of object position,  
575 a major functional characteristic of the dorsal stream. This is congruent with the view that the perception of  
576 variable, less stable object affordances specifically involves the dorsal stream (Sakreida et al., 2016;  
577 Derbyshire, Ellis, & Tucker, 2006). Thus, our selective SMA activation suggests a stronger embodiment of  
578 thematically related object pairs, via the recruitment of the dorsal stream, as the position of objects changes  
579 and the explicit perception of their paired-affordance becomes more difficult. Furthermore, we found  
580 evidence supporting a ventral stream contribution to paired- object affordance processing. Whole brain and  
581 ROI analyses provided converging results showing stronger activation of the left LOC when perceiving  
582 object correctly positioned for action, except in one condition when participants performed a perceptual  
583 action-irrelevant task on pairs of unrelated objects (i.e., context decisions, unrelated objects).

584         This finding is overall consistent with previous fMRI studies that reported increased activity in the  
585 LOC when perceiving objects positioned to interact (Roberts & Humphreys, 2010; Kim & Biederman,  
586 2011). In particular, Roberts & Humphreys (2010) observed an effect of object positioning for action in the  
587 LOC bilaterally regardless of whether the action relation between the two objects was plausible or not (e.g.,  
588 pitcher positioned above glass or above nail), corroborating the claim of a direct, automatic perception of  
589 paired affordance in the ventral stream. Like Roberts & Humphreys (2010), perceiving unrelated objects  
590 correctly positioned for action for right-handed participants also recruited the LOC in our study. However,  
591 the effect observed was less automatic as previously reported. Specifically, the relevance for action of the  
592 task was able to nuance LOC involvement in coding paired-affordances between objects, related or not.  
593 Performance of a perceptual task that did not orient towards action-related features, such as judging object

594 typical context, overruled left LOC greater activation for unrelated objects correctly positioned for action.  
595 This suggests that the LOC codes paired-affordances in a task-dependent manner.

596 Several recent findings support the hypothesis that the LOC represent object features that are  
597 relevant for the current, prepared action (Cohen et al., 2009; Gallivan et al., 2013; Milner, 2017; Schubotz  
598 et al., 2014). When preparing an action towards a single object, LOC was found to discriminate the type of  
599 upcoming action that would be executed with the contralateral hand (i.e., reaching vs. grasping), indicating  
600 the LOC cares about how the observer is about to interact with the perceived object (Gallivan et al. 2013).  
601 Using related object pairs (e.g., knife and apple), Schubotz et al. (2014) demonstrated that LOC activation  
602 increased with the number of possible action affordances associated with a pair, but only when the perceived  
603 objects were presented in compatible actions (e.g., peeling an apple with a knife), compared to incompatible  
604 actions (e.g., making the same peeling movement with a pencil and a sharpener). This finding reinforces the  
605 idea that the LOC does not passively stores object action-related features but is instead actively engaged in  
606 the exploitation of paired-object affordances in accordance with action context and task demands. In our  
607 study, the left LOC was shown to take into account different sources of action information of the  
608 environment, namely object relatedness and type of perceptual processing requested when coding object co-  
609 location for action. Increased LOC activation for standard co-location was observed when either the task or  
610 the relation between objects was action-relevant.

611 In summary, this study provides behavioral evidence for context- and task-dependent processing of  
612 paired-object affordances, that is a benefit of correctly positioning objects for action when judging whether  
613 two related objects are typically used together as opposed as when judging whether two related objects are  
614 from the same context. Critically, fMRI results demonstrate a joint contribution of ventral and dorsal cortical  
615 streams to this effect. Anterior regions of the dorsal stream and in particular SMA responded to inadequate  
616 object co-positioning for action, but only when the perceptual task required action decisions. The role of the  
617 dorsal stream in the paired-object affordance effect reported in our study may therefore correspond to motor  
618 imagery and/or motor simulation strategies. Ventral stream regions and in particular the left LOC was also  
619 involved in coding object co-location for action. Importantly, increased LOC activation for objects correctly  
620 positioned for action was observed in all conditions except when neither task demands nor object relatedness  
621 was relevant for action. Together, the findings from the present fMRI study suggest to reconsider the  
622 automaticity of affordance processing for object pairs in both the dorsal and ventral streams. Environmental  
623 constraints and task demands may bias paired-object affordance coding, in line with flexible views of  
624 affordance evocation (e.g., Borghi & Riggio, 2015; Kalénine & Buxbaum, 2015; Sakreida et al., 2016) and  
625 with important cross-talk between the dorsal and ventral visual pathways (e.g., Kravitz, Saleem, Baker,  
626 Ungerleider, & Mishkin, 2013; Milner, 2017).



627

628 **Acknowledgments**

629 IRMaGe MRI/Neurophysiology facility was partly funded by the French program “Investissement  
630 d’Avenir” run by the "Agence Nationale pour la Recherche"; grant "Infrastructure d’avenir en Biologie  
631 Santé" - ANR-11-INBS-0006.

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