

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

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## ARTICLE INFO

### Keywords:

Visual attention  
Action  
Object perception  
Lateral occipital complex  
fMRI

## ABSTRACT

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

## 1. Introduction

Human environment is full of objects and objects are most often perceived in subsets of items grouped along contextual, spatial, and/or functional relationships rather than in isolation. There is now considerable evidence that the perception of object pairs may be facilitated when objects are correctly positioned for action (Borghi et al., 2012; Green and Hummel, 2006; McNair and Harris, 2014; Roberts and Humphreys, 2011; Xu et al., 2015; Yoon et al., 2010). Interest for action-based effects on object perception has increased after Riddoch, Humphreys and colleagues demonstrated the impact of this factor on neuropsychological deficits (Riddoch et al., 2002, 2006). Visual extinction is a neuropsychological syndrome frequently observed after posterior parietal damage, in which patients fail to report the contralesional stimulus when two stimuli are simultaneously presented in the visual field. Yet extinction may be reduced when the two object

stimuli are correctly positioned for action (e.g., hammer and nail in adequate orientation for co-action), as demonstrated by an important series of patient studies (Riddoch et al., 2006). Recovery from visual extinction is not visible for mere associated objects (hammer-mallet), but has been reported, although to a lower extent, for semantically unrelated objects that could possibly participate in a common action (bottle-bucket). Neuropsychological findings show that visual attention of patients with posterior parietal lesions may benefit from action relations between objects. However, the neural locus of this benefit is not evident and may be related to the relatively preserved functioning of more dorsal (e.g., superior parietal lobule, anterior parietal sulcus) and/or more ventral (e.g., posterior temporal) in these patients.

Following the thorough description of extinction phenomena, an important series of studies have further investigated the cognitive and neural mechanisms underlying the facilitation that relevant positioning for action may provide to the perception of object pairs in healthy

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participants using different paradigms (Green and Hummel, 2006; Roberts and Humphreys, 2010; Xu et al., 2015, 2017; Yoon et al., 2010). In one such study (Yoon et al., 2010), pairs of objects that are typically used together (e.g., frying pan and spatula) were visually presented from a first-person perspective to right-handed participants. Object relative position and task were manipulated. Objects could be positioned in a way enabling the co-manipulation of the objects by right-handers, namely the active object on the right (spatula) and the passive object on the left (frying pan), or in a mirror position. Participants were asked to perform two judgement tasks. In the action decision task, they had to decide whether objects would typically be used together whereas in the contextual decision task they decided whether objects were typically found in the kitchen. A control condition, in which objects were unrelated (e.g., frying pan and saw), was used for “no” trials. Results highlighted an interaction between object co-location and task, with a selective advantage of correct co-location for action in the action decision task: Response times on “yes” trials were faster for correctly co-located objects compared to incorrectly co-located objects when processing the action relation between objects, but not when processing their spatial context. Results are unlikely due to familiarity of object pairs since the benefit of correct co-location for action is only visible for this particular type of judgments. The authors attributed the effect to the “direct route” to action that processes the potential for action between objects bypassing the semantic system. The direct route to action is assumed to rely on brain regions of the dorsal stream, including the dorsal premotor and prefrontal cortex (Humphreys et al., 2010) and may thus be involved in processing affordances for single objects as well as affordances for object pairs. However, as we will review next, the very few neuroanatomical findings related to the processing of paired-object affordances do not provide any clear answer to the neural substrate of the effect. Involvement of either dorsal or ventral brain areas has been alternatively reported with different methodologies and different tasks. The present fMRI study aimed at clarifying the neural correlates of the paired-object affordance effect.

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

In contrast, several studies (Kim and Biederman, 2011; Roberts and Humphreys, 2010; but see Baek et al., 2013) demonstrated with different experimental paradigms that object co-location for action may be coded in the lateral occipital complex (LOC). LOC is a key region of the

ventral stream for the recognition of objects (Altmann et al., 2004; Grill-Spector, 2003; Grill-Spector et al., 2001) that is also particularly sensitive to the perception of tools and tool-related actions (see Lingnau and Downing, 2015 for review). In a fMRI study, Roberts and Humphreys (2010) showed that categorization of objects that are correctly co-positioned for action (e.g., pitcher in a pouring position above glass) induced greater activation of the LOC compared to that of objects that are incorrectly positioned for action (e.g., pitcher in a pouring position below glass). Interestingly, the effect remained present when attention was not directed on the objects (categorization task performed on different pictures of the display) and when objects were only weakly semantically related (e.g., pitcher in a pouring position above nail). However, no changes in activation were found in dorsal brain regions.

One way to reconcile the different lines of evidence is to assume that the paired-object affordance effect may have a double origin. Both dorsal and ventral stream regions may contribute to the coding of object co-position for action but differently depending on the existing relations between objects and task demands. In accordance with Kim and Biederman (2011) and Roberts and Humphreys (2010), the LOC may be sensitive to the correct positioning of objects for action regardless of whether they already share a strong semantic relationship, and even when the task does not explicitly orient attention to the action relationship. In contrast, the dorsal involvement in processing action affordances for object pairs may be more dependent upon stimuli and task context. This is growing evidence showing the activation of motor-related cerebral areas during object perceptual processing is not as automatic as previously envisaged (see van Elk et al., 2014 for review). For instance, Wamain et al. (2016) reported a stronger recruitment of the motor neural network during visual object processing, as reflected by enhanced Mu rhythm desynchronization, when the object was presented within reach compared to out of reach, but only when the task required processing its action-related properties. In another EEG study, Natraj et al. (2013) found that the additional presence of a hand near during the processing of object pairs increased early activation of parieto-frontal areas. Using fMRI, Bach et al. (2010) showed that within a large left frontoparietal network recruited during action observation, the relative involvement of each region depended on the relation between the tool and the goal object and on the characteristics of the action task. For instance, maximum activation of the anterior intraparietal sulcus was reported when the task required to judge whether the relative spatial position of a tool and its recipient (e.g., hole puncher on paper) was correct (spatiomotor task) compared to when the task required to judge whether the two objects could be used together to achieve an action goal (functional task). In contrast, greater activation of the middle frontal gyrus was found during both spatiomotor and functional judgements when tool and goal object shared a functional relation compared to when objects were not directly used together (e.g., CD and cassette tape). Together, recent research supports the flexible activation of affordances during the processing of visual objects, with a greater or lower involvement of motor-related regions of the dorsal stream as a function of contextual factors and task characteristics.

The present study aims at highlighting the flexible contribution of dorsal and ventral stream regions to the paired-object affordance effect using fMRI. This neuroimaging method allows both whole-brain and more specific region-of-interest analyses. Thus, the method is best suited to evaluate the possible involvement of a large fronto-parietal dorsal stream (including the intraparietal sulcus as in Xu et al., 2017, but also premotor and motor regions) as well as more focal ventral stream regions (e.g., LOC) in coding affordances for object pairs. The benefit of positioning the two objects in a correct co-location for action (active object on the right for right-handed participants) was investigated as a function of object relatedness (tool-recipient versus unrelated objects) and task (action versus contextual decisions). Following Yoon et al. (2010), but in contrast to Xu et al. (2017), we selected tasks that involve object identification and manipulated the

presence of a semantic relation between objects, two characteristics that are potentially important to test the recruitment of the ventral stream. However, in contrast to Kim and Biederman (2011) and Roberts and Humphreys (2010), we considered the relevance of task and stimuli for action by designing 3D realistic object pictures on the one hand, and by directly contrasting action-relevant and action-irrelevant judgments on the other hand. Context and task demands have both been proved important for affordance perception for single objects and may be critical for the recruitment of the dorsal stream in the perception of paired-object affordances.

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

## 2. Material and methods

### 2.1. Participants

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

### 2.2. Stimuli and procedure in the POA experiment

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

Forty object pairs were designed, 20 were pairs of semantically related objects that are thematically related and co-manipulated (R condition), and 20 were pairs of unrelated objects (UN condition). In the R condition, each pair was designed in reference to a typical right-handed action. One of the two objects was a passive object usually held, but not maneuvered, by the left hand (e.g., pan or desk lamp), and the other was an active object usually held and manipulated with the right hand (e.g., lid or bulb, respectively). In the UN condition, each pair was made of the same passive object as in the R condition, coupled with another manipulable artifact unrelated to the passive object. In both R and UN conditions, half of the pairs was composed of objects typically found in the kitchen (K condition; e.g., pan and lid), and the other half was composed of objects typically found in another context (NK condition; e.g., desk lamp and bulb). Finally, for both R and UN conditions, we manipulated the co-location for action of the two objects. In a first condition, the passive object – that is the one typically held by the left hand during a right-handed action – was presented to the left, and the second object – the active or unrelated object – was presented to the right. Hence, the objects were presented in a standard co-location for a right-handed action (Standard condition). In a second condition, we

applied a symmetrical rotation of the pairs respective to the vertical axis, so that the presentation of the pair was mirrored relative to the Standard co-location. In this second condition, the passive object was hence presented on the right and the second object, active or unrelated, was presented on the left (Mirror condition).

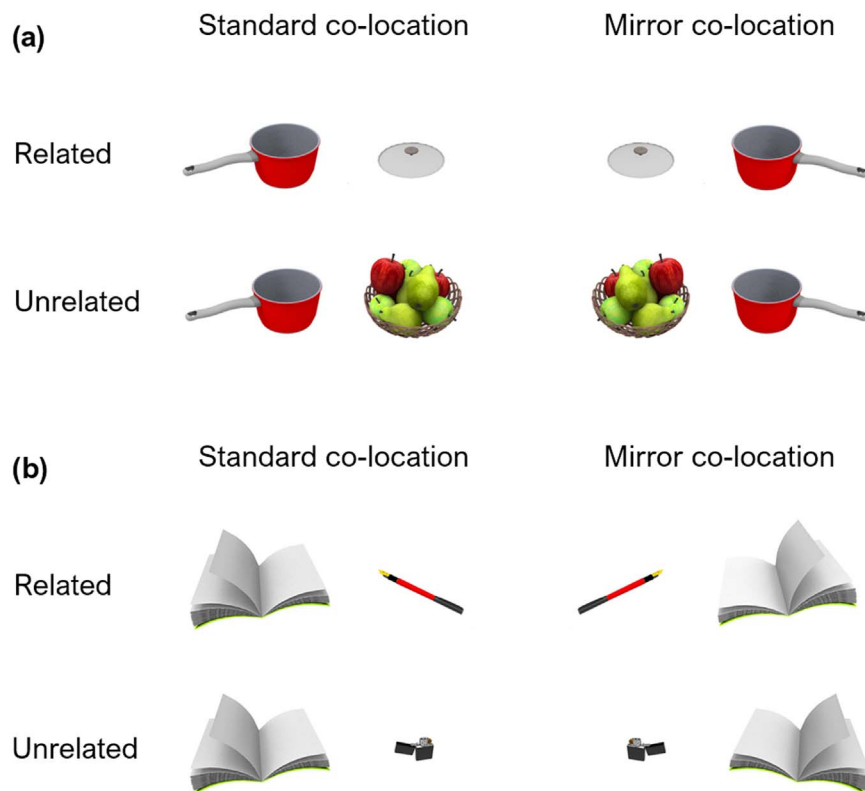
Stimuli were displayed using E-prime software (E-prime Psychology Software Tools Inc., Pittsburgh, USA) and back-projected onto a translucent screen positioned at the rear of the MRI magnet. Participants viewed the screen at a distance of about 222 cm via a mirror fixed on the head coil. After being installed inside the scanner, participants performed two visual tasks: an “Action Decision” task in which they had to decide whether the two objects were typically used together, and a “Contextual Decision” task in which they had to decide whether the two objects were typically found in the kitchen. The order of the tasks was counterbalanced across participants. Participants responded by pressing the keys of a response box disposed inside the scanner with their right hand. One of the response key corresponded to the yes response for the two tasks and the other corresponded to the no response. Half of the participants responded yes with the forefinger and no with the middle finger, and conversely for the other half. Each trial began with the presentation of a central black fixation dot on a white screen for 500 ms, followed by the object pair for 700 ms, and a white screen for 1300 ms, in order to follow an inter-stimuli interval of 2500 ms. Participants were instructed to fixate the center of the screen (fixation dot) and to answer as quickly and accurately as possible as soon as the objects appeared on the screen. For each trial, response accuracy and reaction times (RT, in milliseconds) were recorded. Participants performed a short practice session outside of the scanner with stimuli that were not subsequently used in the experiment.

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

Preliminary tests were performed in order to assess the strength of the thematic relation and of the co-action relation in R and UN pairs. For each pair of objects, eighteen participants who did not participate to the present study judged (1) to what extent the two objects are present in the same context at the same time, even if they are not directly manipulated with each other (thematic judgment), and (2) to what extent the two objects are directly manipulated with each other (co-action judgment). Participants rated their judgements on a 7-point scale from very rarely (level 1) to very frequently (level 7). We calculated mean rating of each participant for R and UN pairs. We then compared ratings of R and UN pairs. A Wilcoxon Signed-Ranks Test indicated that R pairs were judged more strongly thematically-related and co-manipulated than UN pairs (Thematic judgment;  $R = 6.68 \pm .40$ ;  $UN = 2.42 \pm .86$ ;  $Z = 3.72$ ,  $p < .0001$ ; Co-action judgment;  $R = 6.78 \pm .39$ ;  $UN = 1.36 \pm .39$ ;  $Z = 3.72$ ,  $p < .0001$ ).

### 2.3. Stimuli and procedure in the LOC Localizer experiment

Following the main POA experiment, we performed a separate functional LOC Localizer experiment in order to localize the functional regions of interest specifically involved in object visual processing (i.e. the LOC in each hemisphere). The localizer experiment was adapted



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

from previous studies (Kauffmann et al., 2015; Kourtzi et al., 2003; Musel et al., 2014). Participants viewed grayscale images of objects and scenes in separate blocks of a block design paradigm. Stimuli were black-and-white (256 gray-scales) images of objects (manipulable artifacts) and scenes (indoors, beaches, mountains, and cities), all sized to  $256 \times 256$  pixels (or  $6 \times 6$  degrees of visual angle). We designed two other versions of these images: a “square-scrambled” version, made by dividing the intact images into  $21 \times 21$  pixels squares and by randomly spreading them, and a “phase-scrambled” version, made by scrambling the phase of the intact image in the Fourier domain via random permutation, a procedure allowing to preserve the orientation and the spatial frequency content of the images but making impossible to extract any semantic content (Goffaux et al., 2011; Woodhead et al., 2011). The experiment included one functional run. Intact, square-scrambled and phase-scrambled versions of the scene and object images were presented in distinct blocks. The functional run lasted 7 min and 20 s and was composed of 24 15-s task blocks (four blocks of intact objects, four blocks of square-scrambled objects, four blocks of phase-scrambled objects, four blocks of intact scenes, four blocks of square-scrambled scenes, and four blocks of phase-scrambled scenes), each including 15 same type stimuli, interspersed with eight 10-s rest blocks with a fixation dot in the center of the screen displayed against a gray background. Participants performed a ‘one-back’ repetition detection task. They were instructed to press a button whenever they saw two identical stimuli repeated. This task guaranteed that participants paid at least as much attention to the square-scrambled and phase-scrambled stimuli than to the more interesting intact stimuli. Only two repetitions per block were presented. Each stimulus was presented for 300 ms, with a 600 ms interstimulus interval with a fixation dot in the center of the screen. The functional run included 176 functional volumes.

#### 2.4. fMRI acquisition

Experiments were performed using a whole-body 3 T scanner (Achieva 3.0T TX, Philips, NL) with a 32-channel head coil at at

IRMAGE MRI facility (Grenoble, France). For all functional scans of the two experiments, the manufacturer-provided gradient-echo/T2\* weighted EPI method was used. Forty-two adjacent axial slices parallel to the bi-commissural plane were acquired in sequential mode from the bottom to the top, including the cerebellum. Slice thickness was 3 mm. The in-plane voxel size was  $3 \times 3 \times 3$  mm ( $240 \times 240 \times 126$  mm field of view acquired with a  $80 \times 80$  pixel data matrix; reconstructed with zero filling to  $80 \times 80$  pixels). The main sequence parameters were: TR = 2.5 s, TE = 30 ms, flip angle =  $82^\circ$ . Before each functional run, six “dummies scans” were acquired to allow for signal equilibration. Following the seven functional runs (six for the POA experiment and one for the LOC Localizer experiment), a T1-weighted high-resolution three-dimensional anatomical volume was acquired, by using a 3D modified Driven Equilibrium Fourier Transform (MDEFT) sequence (field of view =  $256 \times 224 \times 175$ ; resolution:  $1.333 \times 1.750 \times 1.375$  mm; acquisition matrix:  $192 \times 115 \times 128$  pixels; reconstruction matrix:  $288 \times 288 \times 128$  pixels).

#### 2.5. Data analysis

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

For the main POA experiment, fMRI signal was analyzed using the general linear model (Friston et al., 1995) for event-related design. For each participant, 16 conditions of interest (R-K-Standard, R-K-Mirror, R-NK-Standard, R-NK-Mirror, UN-K-Standard, UN-K-Mirror, UN-NK-Standard, UN-NK-Mirror for the Action Decision and Contextual



Decision tasks) were modeled as 16 regressors convolved with a canonical hemodynamic response function (HRF). For each event, the amplitude of the HRF was adjusted by a parametric modulation based on the response time value of the participant for the corresponding experimental trial. This approach considers the relation between hemodynamic activity and response time, and hence allows to consider the BOLD activity linked to the conditions of interest regardless of the BOLD activity linked to the response execution time. Movement parameters derived from realignment corrections (three translations and three rotations) were also modeled into the design matrix as additional factors of no interest to account for head motion-related variance. Analyses were performed at the individual subject level to examine the different contrasts of interest between estimated parameters of the different experimental conditions. These contrast images were then entered into second-level random effect analyses to test for within group effects (one-sample *t*-tests). The significance of activations was assessed with a statistical threshold of  $p < .001$ , uncorrected for multiple comparisons, with a minimum cluster extent of 10 voxels.

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

### 3. Results

#### 3.1. Behavioral results

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

Global mER was very low ( $7.22 \pm .59\%$ ), indicating that the tasks were easy to perform. The Shapiro-Wilk normality test suggests that the mER were not normally distributed for most of the experimental conditions. Therefore, and because of the low global mER, mER were examined by the mean of a non-parametric test (independence *Khi2*). The main objective of this study was to assess the impact of object co-location for action as a function of the relationship between objects and task demands (action vs. contextual decisions). Thus, we tested the difference in mER between the Standard and Mirror conditions for the R and UN pairs in each task.

For R pairs, results did not show significant difference between Standard and Mirror conditions neither in the Action decision task ( $\chi^2(1, N = 14) = 3.05, p = .08$ ) nor in the Contextual Decision task ( $\chi^2(1, N = 14) = .74, p = .39$ ). Similarly, for UN pairs, there was no difference between Standard and Mirror conditions neither in the Action decision task ( $\chi^2(1, N = 14) = .95, p = .32$ ) nor in the Contextual Decision task ( $\chi^2(1, N = 14) = 1.24, p = .27$ ).

##### 3.1.2. Mean correct responses times (mRT)

The Shapiro-Wilk normality test suggested that mRT were normally distributed for all experimental conditions. A  $2 \times 2 \times 2 \times 2$  repeated-measure ANOVA was conducted on mRT with Task (Action Decision and Contextual Decision), Semantic relation (R and UN), Co-location for action (Standard and Mirror), and Category (K and NK) as within-subject factors. Mean comparisons were explored using planned comparisons and effect sizes were estimated by calculating the partial eta squared ( $\eta^2$ ). Significance level was fixed at  $p < .05$ .

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

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

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

Behavioral results indicated that the advantage of related pairs over unrelated pairs is greater for action decisions than contextual decisions. In addition, the critical pattern of interaction between object co-location for action, object relatedness and task was found. Results highlighted a suppression of the observed cost of correctly positioning pairs of related objects when participants performed action decisions but not contextual decisions. Overall, decisions were slower when the active

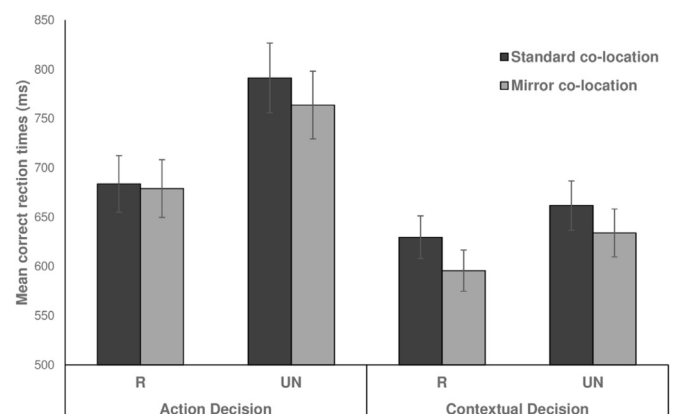


Fig. 2. Mean correct reaction times (milliseconds) as a function of Task (Action Decision vs. Contextual Decision), the semantic relation (Related: R vs Unrelated: UN) and Co-location of objects (Standard vs. Mirror). Errors bars correspond to standard errors.

**Table 1**

Cerebral regions specifically activated for (a) the effect of Task, (b) the effect of Semantic relation, and (c) the effect of object Co-location for each Task and Semantic relation. MNI coordinates (x, y, z) of the peak are indicated. Activations are reported at a statistical threshold of  $p < .001$ , uncorrected for multiple comparisons, and a minimum cluster extent of 10 voxels, except \* $k = 4$ . R = right hemisphere; L = left 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
Middle temporal gyrus	L/R	9	36	3	47	32	4.05
	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>							
No significant cluster	-	-	-	-	-	-	-
<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>							
No significant cluster	-	-	-	-	-	-	-
<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

**Table 1 (continued)**

	Side	BA	k	x	y	z	t
	R	18/ 19	14	18	-91	23	5.26
	L	18	10	-21	-91	14	4.80

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

### 3.2. fMRI results

#### 3.2.1. Whole brain analysis

Since statistical analysis of mER and mRT revealed no effect of category (kitchen versus non kitchen), this factor has not been further considered in the analysis of fMRI data. First, we examined the effect of Task by contrasting activations elicited by Action Decision and Contextual Decision (Table 1). The Action Decision task ([Action > Contextual] contrast) recruited a medial frontal region extending from the anterior cingulate gyrus (BA 32) to the supplementary motor area (BA 6). The Contextual Decision task ([Contextual > Action] contrast) recruited the right middle frontal gyrus (BA 8), as well as the left inferior parietal lobule (IPL, BA 40).

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

Following our hypothesis, we examined the effect of Co-location for action of R and UN pairs in each task (Table 1 and Fig. 3). For R pairs in the Contextual Decision task, the standard co-location of objects ([Standard > Mirror] contrast) activated the left LOC (BA 19/37), and no significant activation was observed for a mirror co-location of objects ([Mirror > Standard] contrast). For R pairs in the Action Decision task, the standard co-location of objects also activated the left LOC. However this time, the mirror co-location of objects activated several regions of the dorsal stream (supplementary motor area, SMA, BA 6; bilateral medial frontal gyrus, BA 9), the bilateral middle temporal gyrus (BA 21) extending in the right parahippocampal gyrus, the left cuneus (BA 17), and the left posterior cingulate gyrus (BA 31). For UN pairs in the Contextual Decision task, the standard co-location activated the left inferior frontal gyrus (BA 45), and the mirror co-location activated the cuneus bilaterally (BA 17/18/19). For UN pairs in the Action Decision task, once again the standard co-location activated the left LOC, and no significant activation was observed for the mirror co-location.

#### 3.2.2. ROIs analysis

The LOC ROIs were defined in each participant based on the independent Localizer experiment, and were used as the structural constraint for the analysis of the data in the POA experiment. The LOC was identified in each hemisphere and in each participant based on the [intact objects > phase-scramble objects] contrast. In each identified region, the activation peaks that best correspond to previous results in the literature (Grill-Spector et al., 2001; Altmann et al., 2004; Roberts and Humphreys, 2010) were selected to create two spherical ROIs independently for each participant (see Fig. 4): the left LOC (mean MNI coordinates and standard deviations:  $x = -39 \pm 5$ ,  $y = -78 \pm 6$ ,  $z = -9 \pm 7$ ) and the right LOC ( $x = 39 \pm 3$ ,  $y = -78 \pm 5$ ,

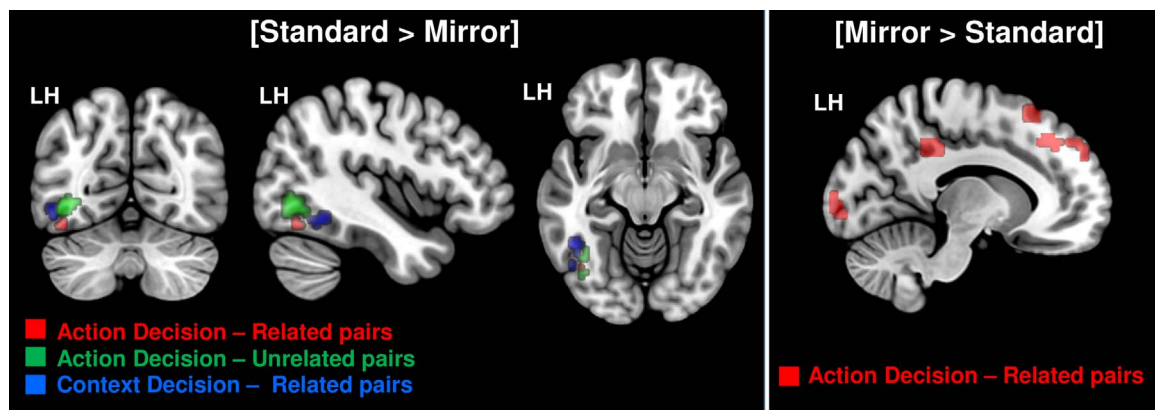


Fig. 3. Effect of object co-location on cerebral activations revealed by [Standard > Mirror] and [Mirror > Standard] contrasts depending on the semantic relation between objects (Related vs. Unrelated) and the task (Action Decision vs. Contextual Decision). LH: left hemisphere.

$z = -8 \pm 5$ ). Parameters estimates (% signal change relative to the global mean intensity of signal) were extracted from the two sphere ROIs for each participant. The average parameter of activity was then calculated for each experimental condition. These values were submitted to a repeated measures ANOVA for each ROI with Task (Action Decision and Contextual Decision), Semantic relation (R and UN), and Co-location for action (Standard and Mirror) as within-subject factors.

For the left LOC, there was a main effect of Semantic relation. UN pairs elicited more activation than R pairs ( $F(1,13) = 11.15$ ,  $p < .05$ ,  $\eta^2 = .46$ ). The main effect of object co-location was also significant. The left LOC was more activated when the two objects were in standard co-location than in mirror co-location ( $F(1,13) = 10.54$ ,  $p < .05$ ,  $\eta^2 = .45$ ). Semantic relation did not interact with Co-location ( $F(1,13) = 1.62$ ,  $p = .22$ ), but these variables interacted with Task ( $F(1,13) = 4.80$ ,  $p < .05$ ,  $\eta^2 = .27$ ). For R pairs, the Standard co-location of objects elicited more activation than the Mirror co-location both in the Action Decision task ( $F(1,13) = 6.34$ ,  $p < .05$ ) and in the Contextual Decision task ( $F(1,13) = 13.94$ ,  $p < .05$ ). For UN pairs, the Standard co-location of objects elicited more activation than the Mirror co-location in the Action Decision task ( $F(1,13) = 7.17$ ,  $p < .05$ ), but not in the Contextual Decision task ( $F(1,13) < 1$ ).

For the right LOC, there was also a main effect of Semantic relation ( $F(1,13) = 29.00$ ,  $p < .001$ ,  $\eta^2 = .69$ ). UN pairs elicited more activation than R pairs. The main effect of Task was also significant ( $F(1,13) = 5.33$ ,  $p < .05$ ,  $\eta^2 = .30$ ). The right LOC was more activated in the Action decision task than in the Contextual decision task.

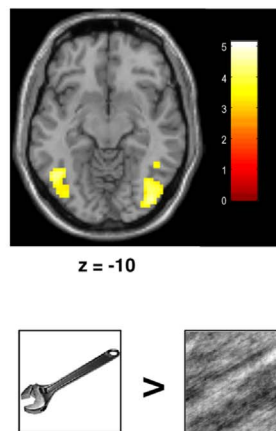
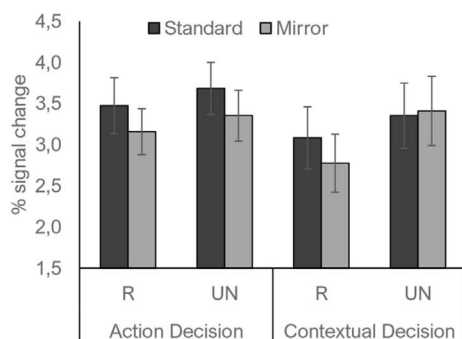
However, the main effect of object co-location was not significant ( $F(1,13) < 1$ ). Interactions did not reach significance in the right LOC, neither between Semantic relation and co-location of objects ( $F(1,13) = 3.63$ ,  $p = .08$ ), nor between Task, Semantic relation, and co-location of objects ( $F(1,13) = 3.14$ ,  $p = .10$ ).

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

#### 4. Discussion

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

(a) Left lateral occipital complex (LOC)  
(-39x, -78y, -9z)



(b) Right lateral occipital complex (LOC)  
(39x, -78y, -8z)

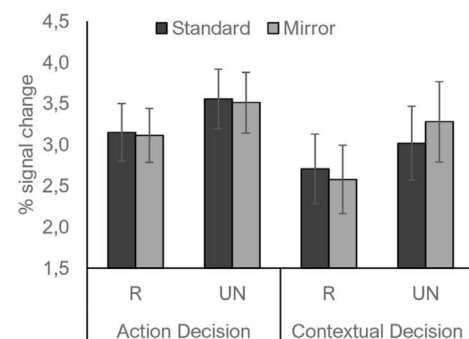


Fig. 4. Bilateral activation of the Lateral Occipital Complex (LOC) during the perception of object pairs illustrated on a representative participant. The LOC ROIs were defined independently for each participant by contrasting intact objects to phase-scrambled objects: [Intact Objects > Phase-Scrambled Objects]. Parameters estimates were then extracted from ROIs for each participant and each experimental condition: Task (Action Decision vs. Contextual Decision), Semantic relation (Related-R vs. Unrelated-UN), and object Co-location (Standard vs. Mirror). Graphs represent the mean percentage of signal change for each ROI. Error bars correspond to standard errors.

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

Regarding the effect of co-location for action, results first showed a processing cost of the standard co-location for related pairs in the particular case of contextual decisions. One possibility is that the presentation of closely related objects entails automatic processing of paired object affordances, drawing visual attention on object properties that are not fully relevant for the current task, namely determining whether the two objects are typically found in the kitchen. Such a processing cost was not reported by Yoon et al. (2010). They found no statistical difference between standard and mirror co-locations of related objects in the Contextual decision task, but RTs were descriptively longer for standard co-locations. In the present study, a similar processing cost was also observed for unrelated pairs in both tasks. Although this cost was rather unexpected, the direction of the effect of object co-location for unrelated pairs was difficult to predict a priori. In Yoon et al. (2010), unrelated object pairs (“no” responses) were analyzed separately and were not sensitive to the effect of object co-location for action. The reason why participants were slower to process unrelated object pairs presented in standard co-location in our study remains unclear. One possible interpretation is related to individual objects properties. Many passive objects of our stimuli base (e.g., pan, cup, glass, bottle, etc.) may individually elicit stronger motor affordances than unrelated objects (e.g., ashtray, vessel, bin, alarm clock, etc.) especially when positioned on the right, matching a right hand holding the object as in the mirror co-location condition. Passive objects of unrelated pairs could thus have been mostly treated individually rather than as in a pair, disrupting the two tasks based on the processing of both objects.

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

Although the general neural substrates of thematic relations was not the focus of the present study and the comparison between related and unrelated pairs was possibly contaminated by task demands, we verified that processing of thematically-related objects involved the cortical network previously reported in the literature. This network includes the temporo-parietal junction, the IPL, and the posterior part of the middle and superior temporal gyri, mainly in the left hemisphere (de Zubicaray et al., 2013; Kalénine et al., 2009; Kalénine and Buxbaum, 2016; Sass et al., 2009; Schwartz et al., 2011; Tsagkaridis et al., 2014). The related vs. unrelated contrast indeed revealed a

cluster of activation in the posterior part of the left temporo-parietal cortex. Furthermore, when we examined the cortical regions differently involved in the two judgment tasks, results showed that contextual judgments, compared to action judgments, recruited the left IPL. Considering that contextual decisions required the explicit search of thematic connections between objects in relation to the kitchen context, the left IPL may be specifically involved in this process, regardless of whether a thematic relation is actually present or not (related and unrelated pairs). These results thus provide additional evidence for an important role of the posterior parieto-temporal cortex in the processing of thematic relations.

Action judgements compared to contextual judgments activated the supplementary motor area (SMA), a brain region typically involved in action processing and found to play a crucial role in bimanual movement coordination (Sadato et al., 1997; Serrien et al., 2002). In addition, a recent fMRI meta-analysis on over 60 research articles (Héту et al., 2013) reported a constant activation of the SMA, among other frontal regions (e.g., middle and inferior frontal gyrus), for tasks involving motor imagery. These frontal regions were found in particular for upper limbs motor imagery and for objects-directed actions. Therefore, it is likely that action decisions (i.e. deciding if the two objects are typically used together) involve motor imagery strategies recruiting medial frontal regions like the SMA.

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



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

The selective contribution of the dorsal stream to the explicit processing of paired-object affordances when objects are presented in a difficult position for their use is consistent with the hypothesis of a joint but flexible involvement of dorsal and ventral brain areas in affordance processing (Binkofski and Buxbaum, 2013; Buxbaum and Kalénine, 2010; Kalénine and Buxbaum, 2015; Rizzolatti and Matelli, 2003). The potential for co-action of related objects is largely dependent upon object semantics (i.e. object typical use), which involves the ventral stream processing. Therefore, the recruitment of the dorsal stream during the identification of familiar thematic relations between objects is probably minimal in regular circumstances (e.g. standard co-location). Yet the identification of the same familiar relations when objects are not in a regular position would require additional online spatio-motor transformations of object position, a major functional characteristic of the dorsal stream. This is congruent with the view that the perception of variable, less stable object affordances specifically involves the dorsal stream (Sakreida et al., 2016; Derbyshire et al., 2006). Thus, our selective SMA activation suggests a stronger embodiment of thematically related object pairs, via the recruitment of the dorsal stream, as the position of objects changes and the explicit perception of their paired-affordance becomes more difficult. Furthermore, we found evidence supporting a ventral stream contribution to paired-object affordance processing. Whole brain and ROI analyses provided converging results showing stronger activation of the left LOC when perceiving object correctly positioned for action, except in one condition when participants performed a perceptual action-irrelevant task on pairs of unrelated objects (i.e., context decisions, unrelated objects).

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

Several recent findings support the hypothesis that the LOC represent object features that are relevant for the current, prepared action (Cohen et al., 2009; Gallivan et al., 2013; Milner, 2017; Schubotz et al., 2014). When preparing an action towards a single object, LOC was found to discriminate the type of upcoming action that would be executed with the contralateral hand (i.e., reaching vs. grasping), indicating the LOC cares about how the observer is about to interact with the perceived object (Gallivan et al., 2013). Using related object pairs (e.g., knife and apple), Schubotz et al. (2014) demonstrated that LOC activation increased with the number of possible action affordances associated with a pair, but only when the perceived objects were presented in compatible actions (e.g., peeling an apple with a knife),

compared to incompatible actions (e.g., making the same peeling movement with a pencil and a sharpener). This finding reinforces the idea that the LOC does not passively store object action-related features but is instead actively engaged in the exploitation of paired-object affordances in accordance with action context and task demands. In our study, the left LOC was shown to take into account different sources of action information of the environment, namely object relatedness and type of perceptual processing requested when coding object co-location for action. Increased LOC activation for standard co-location was observed when either the task or the relation between objects was action-relevant.

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

## Acknowledgments

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

## Declarations of interest

None.

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