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The involvement of the dorsal stream in processing implied actions between paired objects: A TMS study

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1 **The involvement of the dorsal stream in processing implied**

2 **actions between paired objects: a TMS study**

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Abstract: Perceiving and selecting the action possibilities (affordances) provided by objects is an important challenge to human vision, and is not limited to single-object scenarios. Xu, Humphreys and Heinke (2015) identified two effects of implied actions between paired objects on response selection: an inhibitory effect on responses aligned with the passive object in the pair (e.g. a bowl) and an advantage associated with responses aligned with the active objects (e.g. a spoon). The present study investigated the neurocognitive mechanisms behind these effects by examining the involvement of the ventral (vision for perception) and the dorsal (vision for action) visual streams, as defined in Goodale and Milner's (1992) two visual stream theory. Online repetitive transcranial magnetic stimulation (rTMS) applied to the left anterior intraparietal sulcus (aIPS) reduced both the inhibitory effect of implied actions on responses aligned with the passive objects and the advantage of those aligned with the active objects, but only when the active objects were contralateral to the stimulation. rTMS to the left lateral occipital areas (LO) did not significantly alter the influence of implied actions. The results reveal that the dorsal visual stream is crucial not only in single-object affordance processing, but also in responding to implied actions between objects.

2

1. Introduction

In his seminal book, Gibson (1979) postulated that humans directly detect action possibilities (affordances) from the physical properties of objects in an automatic fashion. There is now substantial evidence for this claim (e.g. Bub, Masson, & Cree, 2008; Phillips & Ward, 2002; Riddoch, Edwards, Humphreys, West, & Heafield, 1998; Riddoch, Humphreys, Edwards, Baker, & Willson, 2003; Tucker & Ellis, 1998). For instance, despite being irrelevant to the task, responses are speeded when they are compatible with the grasping action afforded by a visual object, while those incompatible with the action are slowed down (e.g. Ellis & Tucker, 2000; Phillips & Ward, 2002; Tucker & Ellis, 1998).

Extending the line of studies which examined affordance extraction in single, isolated objects, recent studies revealed that the automatic extraction of action-related information is not confined to single objects, but extends to visual scenarios in which pairs of objects are presented (e.g. Humphreys, Wulff, Yoon, & Riddoch, 2010; Humphreys, Yoon, et al., 2010; Riddoch, et al., 2003; Roberts & Humphreys, 2010a, 2010b, 2011a, 2011b). In these studies, participants see object pairs where one object is "active" while the other object is "passive". Active objects (e.g. a spoon in a spoon-bowl pair) are those items used in the action between the objects (e.g., grasping and scooping from the bowl), while the passive objects only need "stabilization" (e.g., the bowl in the spoon-bowl pair, see Figure 1). In a series of studies with such stimuli, Riddoch and colleagues reported that, for patients with extinction, positioning objects

1 for action enabled the patients to attend to both members of a pair, alleviating the

2 impairment in detecting contralesional items (Riddoch, et al., 2003). In normal

3 observers, correctly co-locating objects for action, compared with when they are

4 incorrectly co-located for action, facilitated object identification (Roberts & Humphreys,

5 2011b), and correctly co-located objects induce a bias towards identifying the active

6 objects relative to the passive objects in each pair (Roberts & Humphreys, 2010b).

7 However, so far the neural correlates of between-object affordance processing is not

8 fully understood. Especially, there is no causal evidence from healthy participants

9 regarding the neural correlates of affordance processing of implied actions between

10 objects, and the present study aims to provide such causal evidence using transcranial

11 magnetic stimulation (TMS).

12 Two hypotheses for the neural correlates can be motivated from previous

13 literature: the ventral stream or/and the dorsal stream hypotheses. The dorsal stream

14 hypothesis is supported by theories distinguishing vision for action (through the dorsal

15 stream) from vision for perception (through the ventral stream, for reviews, see

16 Goodale & Milner, 1992; Milner & Goodale, 2006, 2008; see also Riddoch,

17 Humphreys, & Price, 1989; Yoon, Heinke, & Humphreys, 2002). Within the framework

18 of these theories, affordance-related processing is generally attributed to the dorsal

19 visual stream. However, the evidence for the involvement of the dorsal pathway in

20 affordance-based processing mainly stems from experiments using single objects

21 (e.g. Chao & Martin, 2000; Grèzes & Decety, 2002; Valyear, Culham, Sharif,

Westwood, & Goodale, 2006; for review, see Lewis, 2006). The question arises whether the affordance processing of the dorsal pathway also extends to the processing of affordance implied by object pairs.

On the other hand, the ventral stream hypothesis has been supported by direct evidence that the ventral stream is involved in affordance processing of object pairs. In particular, Roberts and Humphreys (2010a) reported enhanced activation in the ventral visual stream including the lateral occipital complex (LOC) and fusiform gyrus, for pairs of objects that were correctly positioned for action compared with objects incorrectly positioned for action. Roberts and Humphreys argued that action-positioned objects could trigger a visual recognition response within the ventral stream, facilitating the grouping of action-related objects (see also Kim & Biederman, 2011 for evidence pointing in the same direction). The ventral stream areas including the lateral occipital and temporal regions are also implicated in the perception of tools and their usage (Johnson-Frey, 2004; Lingnau & Downing, 2015), naming pictures of tools (e.g. Chao, Haxby, & Martin, 1999; Martin, Wiggs, Ungerleider, & Haxby, 1996), tool manipulation (Perini, Caramazza, & Peelen, 2014) and naming of actions performed with tools (Damasio, et al., 2001). The LOC may play a role in the recognition of such objects and action relation between them, when presented in pairs. Finally, it is important to point out that evidence on affordance processing of object pairs is largely based on brain imaging studies and is thus largely correlational. Though there are also neuropsychological studies based on patient data (e.g.

1   Humphreys, Riddoch, & Fortt, 2006; Riddoch, et al., 2006; Riddoch, et al., 2003), the

2   patients in these studies tend to have extensive lesions covering both the

3   ventral-stream temporal areas and the dorsal-stream parietal areas. Consequently, it

4   remains unclear whether the contribution from either visual stream, or both, is a

5   prerequisite for processing of implied between-object actions.

6   To causally test these two hypotheses, the present study uses online repetitive

7   transcranial magnetic stimulation (rTMS) to induce a "virtual lesion" to representative

8   areas of each stream, the left anterior intraparietal sulcus (aIPS) and the left lateral

9   occipital cortex (LO) for the dorsal and the ventral pathway respectively. As a

10   representative region within human ventral visual stream, the lateral occipital complex

11   (LOC), composed of the lateral occipital cortex (LO) and the posterior fusiform gyrus

12   (pFs), has been reported to be activated in human neuroimaging studies across a

13   range of object perception and recognition tasks (for review, see Grill-Spector, Kourtzi,

14   & Kanwisher, 2001), and showed selectivity to tool- and hand- stimuli (for review, see

15   Lingnau & Downing, 2015). TMS to the Left LO (Brodmann's area 37) slows subjects'

16   reactions for object naming (Stewart, Meyer, Frith, & Rothwell, 2001) and stimulation

17   to the right LO affects shape discrimination (Ellison & Cowey, 2006) and tool

18   manipulation judgements (Perini, et al., 2014). The left LOC was also activated by

19   viewing action-related objects in Roberts and Humphreys (2010a). As a representative

20   region within the human dorsal visual stream, the aIPS has been proposed to mediate

21   online control of object-directed grasping (Binkofski, et al., 1998; Culham, et al., 2003;

1   Frey, Vinton, Norlund, & Grafton, 2005; Rice, Tunik, Cross, & Grafton, 2007; Tunik,

2   Frey, & Grafton, 2005). Further, a left-lateralized network of brain regions including the

3   aIPS was identified (i) during studies in which there was increased activation for tools

4   compared to other objects (Chao & Martin, 2000; Chouinard & Goodale, 2012;

5   Mruczek, von Loga, & Kastner, 2013; Valyear, Cavina-Pratesi, Stiglick, & Culham,

6   2007) and (ii) during viewing, hearing, executing, planning, and pantomiming tool use

7   (Lewis, 2006), in which tool use actions are preferred compared to control conditions.

8   TMS over the left aIPS has also been reported to affect online grasping (Cohen, Cross,

9   Tunik, Grafton, & Culham, 2009).

10   During the stimulation, we engaged the participants in a behavioural task devised

11   by S. Xu et al. (2015). In S. Xu et al.'s (2015) task two objects were simultaneously

12   presented on the screen, one on the left and one the right side (see Figure 1). They

13   were either correctly positioned for interaction (e.g., a spoon was positioned with its

14   scooping end towards a bowl, see Figure 1a) or not (e.g., a spoon was positioned with

15   its scooping end pointing upwards and away from a bowl, see Figure 1b).

16   Subsequently a small shape, circle or triangle, was added at the centre of the screen

17   and the participants were asked to make speeded left/right keyboard responses

18   indicating which of the shapes was presented. Importantly, the responses were

19   aligned with either object in the object pair. Hence, and in contrast to most previous

20   studies on between-object affordance, not only the implied action relationship but also

21   the objects were task irrelevant (though see Roberts & Humphreys, 2010a).

1   Nevertheless, S. Xu et al. (2015) showed that in this paradigm the objects affected

2   participants' responses in two ways. First, they found that responses were quicker if

3   they were aligned with the active objects compared with the passive objects—a

4   facilitation effect—when the two objects were positioned as if in interaction. Second

5   and in addition to this facilitation effect, the responses aligned with the passive objects

6   were slower when the two objects were presented as if in interaction, compared with

7   when they were not in interaction. Collectively, these two effects produced an

8   interaction between co-location and response compatibility. S. Xu et al. (2015)

9   interpreted these findings as evidence for affordance-based response selection (e.g.

10   Cisek, 2007; Thill, Caligiore, Borghi, Ziemke, & Baldassarre, 2013) when viewing

11   action-related object pairs: initially the affordances of both objects are extracted (e.g.

12   handles and other action-relevant object parts) and are subsequently entered into a

13   competition for a motor response, in which the active object wins, and the response to

14   the passive object is inhibited since it is incompatible with the action collectively

15   afforded by the object pair. In addition, with a series of control experiments, S. Xu et al.

16   (2015) demonstrated that when the orientation of the passive objects, instead of the

17   active objects, were manipulated in the incorrect co-location condition, the interaction

18   between co-location and response compatibility and the inhibition of the passive

19   objects vanished (the advantage of the active objects remained, which makes sense

20   since the correct co-location condition was identical to the experiment where the

21   effects of implied between-object actions were initially reported), though the size and

22   shape difference between the active and the passive objects were kept constant,

8

suggesting that response selection in paired-object scenarios is influenced by affordance-related processes and cannot be exclusively ascribed to experimental manipulations such as size or orientation differences between objects. Also, S. Xu et al. (2015) demonstrated that when the paired-object scenario was reduced to single-object scenarios by leaving the space used to be occupied by the passive objects empty, both the advantage and the inhibition effects disappeared. These findings demonstrate that the two effects, as well as the interaction between co-location and response compatibility, are ideal indices of TMS effect on affordance-based processing of implied between-object actions. We predict that rTMS, used to suppress neural activity, reduces the advantage of the active objects and the inhibition of the passive objects when rTMS is applied over areas critical to the between-object-affordance effects. We also included a neutral TMS condition (stimulation given over the vertex) to control for the general, non-specific effects of stimulation.

2. Materials and Methods

2.1. Design

The experiment followed a 2 (co-location: correct vs. incorrect) × 2 (the layout of paired objects: active-left vs. active-right) × 2 (response compatibility: active object vs. passive object) × 3 (Stimulation site: Cz, left aIPS & left LO) within-subject factorial design.

2.2. Participants

Twenty-two healthy volunteers (7 females, age range 18-25 years) with no previous history of neurological problems or contraindication to TMS participated. All participants had normal or corrected-to-normal vision and were right handed. Participants gave informed consent and received monetary compensation for their time. The present research was approved by the local ethics committee at the University of Birmingham.

2.3. Apparatus

The experiment was run on a Windows PC with a 1GMHZ Pentium III processor, using a Philips 109S monitor (1280 × 1024 at 75 Hz). Matlab7 (The MathWorks Inc., Natick, MA, USA) with Psychtoolbox 3 was used to display the stimuli and record RTs.

2.4. Stimuli

The stimuli consisted of 23 pairs of line-drawing images of objects on a light grey (200, 200, 200 RGB) background. Each pair included an active object and a passive object commonly used together in actions (see Figure 1 for an example and Table S1 in supplementary materials for a complete list of the object pairs used). Some stimuli appeared in more than one object pair. For instance, a jug appeared in a jug-cup pair and a jug-glass pair. In total, 16 active objects and 15 passive objects were used as stimuli. Each object image subtended 3.2°×3.2° of visual angle. The relative sizes of the objects within each pair matched their relative sizes in real life. Other stimuli included a fixation cross subtending 0.8°×0.8° of visual angle and two blue (0, 121, 212

10

1   RGB) response targets (a triangle or a circular disk), both subtended 0.6°×0.6° of

2   visual angle.

3   The stimuli were rated by two different participant groups with respect to (a)

4   whether the action relations between the objects were familiar and apparent, (b)

5   whether, by changing the orientation of the active objects in the incorrect co-location

6   condition, we effectively manipulated the implied actions between objects, (c) whether

7   the objects always afford actions by the hand aligned to their location, and (d) the

8   appropriateness of our assignment of active and passive objects. The results revealed

9   that the stimuli satisfied these criteria. A detailed description of the procedure and the

10   results of the stimulus evaluation process can be found in our previous paper (S. Xu et

11   al., 2015, supplementary materials).

12 **2.5. Procedure**

13   The participants were seated in a comfortable chair, with their chins resting on a

14   chin rest, and the index and the middle fingers of their right hand resting on the j and k

15   keys respectively. Each test session consisted of one practice block and five

16   experimental blocks. The practice block consisted of 64 trials, randomly assigned to

17   different conditions. Each experimental block consisted of 64 trials following one

18   warm-up trial. The experimental trials were evenly assigned to different conditions and

19   were presented in a pseudo-randomized order, with no more than three consecutive

20   trials from the same condition. Each warm-up trial was randomly assigned to a

21   condition. The testing of each participant was divided into three days. On each day the

1   participants took part in one TMS stimulation condition. The order of stimulation sites

2   was varied across participants.

3   On each trial, line-drawings of two objects were presented on the screen. On half

4   of the trials (in the correct co-location condition), the pair of objects were co-located

5   appropriately for interaction (e.g. a spoon was positioned with its scooping end

6   towards a bowl, Figure 1a). On the other half of the trials (the incorrect co-location

7   condition), the active object was positioned in an orientation inappropriate to interact

8   with the corresponding passive object, while the orientation of the passive object was

9   maintained relative to the correct co-location condition (e.g., a spoon was positioned

10 with its scooping end pointing upwards and away from the bowl besides it, Figure 1b).

11 In the active-left condition, the active objects were presented on the left side of the

12 screen, while the passive objects appeared on the right side. In the active-right

13 condition, the whole presentation was horizontally flipped from the corresponding

14 active-left presentation.

	Active objects on the left	Active objects on the right	
a			Correct co-location
b			Incorrect co-location
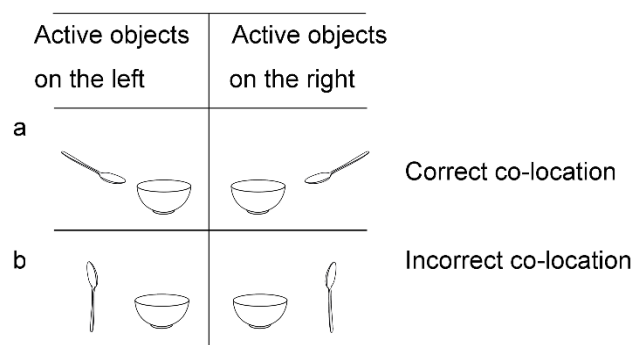
15

16 Figure 1. Examples of the stimuli used in the experiments.

17

1   At the beginning of each trial, a fixation cross was presented at the center of the

2   screen for 400 ms. After this the fixation cross disappeared and the object pair

3   appeared. After 240ms or 400ms a central target was presented (see Figure 2). The

4   majority of the trials (75% of all) were with a 240ms SOA. The number of trials with

5   400ms SOA were reduced compared to the original procedure (S. Xu et al., 2015) in

6   order to shorten the length of sessions while at the same time mimicking the variation

7   of SOA, as in our previous experiments. This variation may prevent participants from

8   responding to the central target at a constant "rhythm". Such a response rhythm may

9   have cancelled out the effect of the implied actions between objects pairs on response

10   times (e.g. Grosjean, Rosenbaum, & Elsinger, 2001). The 400 ms SOA trials were

11   treated as filler trials.

1
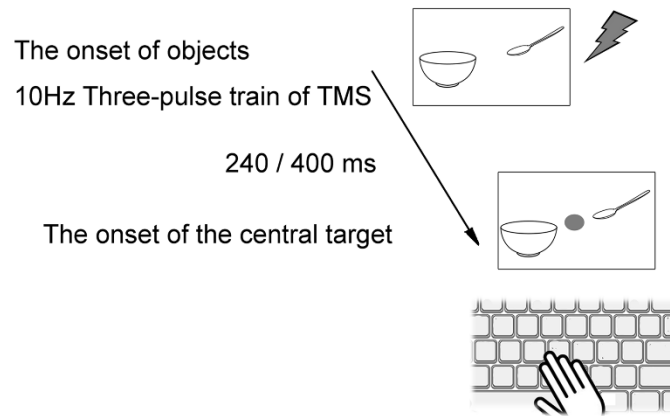
Figure 2. The procedure on a typical trial. The participants were required to make

speeded key-press responses with the index or the middle finger of the right hand,

according to the shape of the central target (shown in light grey in display 2). The

responses made by the finger on the same side with the active objects (middle-finger

responses in this figure) were considered aligned with the active objects and responses

on the other side (index-finger responses in this figure) were aligned with the passive

objects.

The target and the object pair remained on the screen until the participants made

a response or 1600 ms passed without a response. Participants indicated whether the

target was a triangle or a circle by using their index and the middle fingers of the right

hand to press the j or the k key on a QWERTY keyboard. The stimulus–response

mapping was counter-balanced across subjects. The participants were required to

respond as quickly and accurately as possible, and feedback was given immediately

when they failed to make responses within 1600ms after the target's onset or an

incorrect response was made. The responses were assigned to the fingers of the

same hand to avoid an influence from the difference between responses made by the

dominant and the non-dominant hands. Also note that S. Xu et al. (2015) have

1 demonstrated the two effects of implied between-object actions with single-hand

2 responses.

3   As in our previous study, we assessed the effects of implied between-object

4 actions by comparing the correct co-location condition with the incorrect co-location

5 condition (baseline). For example, take the correct co-location condition when the

6 active objects were presented on the left side (left panel in Figure 1a). Here a right

7 response to the shape would be aligned with a response afforded by the passive object

8 (the bowl). Whether the implied between-object actions modulated this response was

9 tested by comparing responses against a baseline when a right response was required

10 and the orientation of the active object (the spoon) was incorrect for any interaction

11 between the objects (left panel, Figure 1b).

12   In this study, we always presented the passive objects in their typical orientation,

13 but varied the orientation of the active objects to manipulate the co-location between

14 objects. The contrast across the co-location conditions on the responses aligned with

15 the passive objects (slowed down in the correct co-location condition), along with the

16 interaction between co-location and response compatibility, provides robust evidence

17 for the inhibitory effects of the implied actions between objects on responses evoked

18 by the passive objects (S. Xu et al., 2015). This effect is treated as one contrast of

19 interest in the analysis of the present study. A second contrast of interest is the

20 advantage of the active objects compared to the passive objects in the correct

21 co-location condition.

2.6. rTMS Procedure

A Magstim Rapid stimulator (MagStim, Whitland, UK) with a 70-mm figure 8 coil was used to deliver TMS to three cortical sites: (1) the most anterior region of the IPS in the left hemisphere (aIPS), (2) the lateral occipital cortex (LO) in the left hemisphere, and (3) Vertex as a control site. A high-resolution three-dimensional volumetric structural magnetic resonance image (MRI) was obtained for each subject (3T magnetic resonance imaging scanner; Philips, Aachen, Germany), and the cortical surface was displayed as a three-dimensional representation using Brainsight Frameless Stereotaxic software (Rogue Research, Montreal, Quebec, Canada). The aIPS and the LO, defined for each participants separately as described below, was demarcated on his or her three dimensional image using the same software. The position of the coil and the subject's head were monitored using a Polaris Optical Tracking System (Northern Digital, Waterloo, Ontario, Canada). Positional data for both rigid bodies were registered in real time to a common frame of reference and were superimposed onto the reconstructed three-dimensional MRI of the subject using the Brainsight software (Rogue Research). Thus, the center of the coil (the stimulation locus) was continuously monitored to be over the site of interest. For all sites, the TMS coil was held tangential to the surface of the skull. An adjustable frame was used to hold the TMS coil firmly in place, while the participants rested their heads on the chin rest. Head movements were monitored constantly by Brainsight and were negligible.

1   Stimulation intensity was set at 60% of the maximum intensity of the stimulator. On

2   each trial, the participants received a 10-Hz train of three pulses simultaneous with the

3   onset of the object pair. The stimulation intensity can be set according to the individual

4   motor threshold of a participant. However, Stewart, Walsh and Rothwell (2001)

5   demonstrated that the motor threshold is not related to the excitability of the visual

6   cortex. Therefore we held the stimulation intensity constant across participants.

7   Stimulation levels and protocols same or similar to that used in the present study have

8   been shown to be sufficient to produce disruptive stimulation effects in sensory and

9   association cortices (e.g. Striemer et al. 2011; for similar protocols see 5 pulses at 10

10   Hz in Mevorach et al. 2010; 5 pulses at 10 Hz in Chang et al. 2014; 3 pulses at 20 Hz in

11   Mevorach et al. 2009). We used 3 pulses in each train of stimulation to ensure that the

12   motor response does not coincide with stimulation.

13   **2.7. Localization of brain sites for TMS**

14   *LO*[1] A full-brain high-resolution anatomical image along with a region of interest

15   localiser imaging data were acquired for each participant at the Birmingham University

16   Imaging Centre using a 3-tesla Philips MRI scanner with an eight-channel head coil.

17   Blood oxygen level–dependent signals were measured with an echo-planar sequence

18   (TE 35 ms; TR 2000 ms; 2.5 × 2.5 × 3 mm, 32 slices). fMRI data were analyzed with

19   BrainVoyager QX (Brain Innovation, B.V.). For each participant, we transformed the

anatomical data into Talairach space. Functional data were preprocessed using

three-dimensional motion correction, slice time correction, spatial smoothing (5 mm),

linear trend removal and high-pass filtering (three cycles per run cut-off). The lateral

occipital cortex (LO) was defined using a standard localizer experiment. In this

experiment, the participants viewed intact and scrambled images of grayscale photos

and line drawings of objects. The LO was defined as the set of voxels in lateral

occipito-temporal cortex which responded significantly (p < 10e-4) more strongly to

intact than scrambled images of objects (see Preston, Kourtzi, & Welchman, 2009 for

details). The average Talairach coordinates of the LO was [-43, -66, -4], with 95% CI

[-45, -41], [-69, -63], and [-6, -2], respectively.

aIPS We localized the aIPS by structural landmarks, i.e. the junction between the

anterior extent of the IPS and the inferior postcentral sulcus, on individual anatomical

images. This was shown to be effective in defining the aIPS (Cohen, et al., 2009;

Davare, Rothwell, & Lemon, 2010; Rice, Tunik, & Grafton, 2006). Stimulation loci were

superimposed onto the reconstructed three-dimensional MRI image of each subject

using the Brainsight software. The average Talairach coordinates of the aIPS were

[-37, -39, 41], with 95% CI [-39, -35], [-42, -37], and [38, 44], respectively. This is within

the confidence range of the left aIPS collated from recent fMRI studies which reported

activation in the aIPS in action/grasping related tasks (Frey, et al., 2005).

Cz was defined individually by the point of the same distance to the left and the

right pre-auriculars, and of the same distance to the nasion and the inion.

1
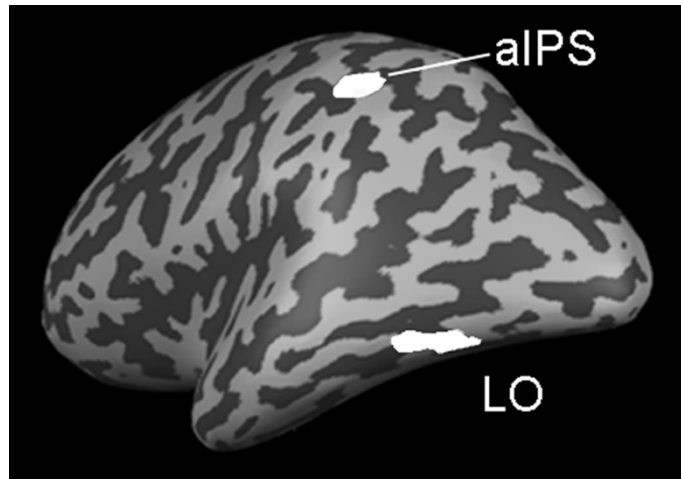
2 Figure 3. Stimulation sites. A three dimensional inflated rendering of one subject's

3 structural MRI in BrainVoyager QX, illustrating the cortical sites chosen for stimulation.

4 White areas: the left aIPS and the left LO.

5

6 3. Results

7   Participants were highly accurate, with the average accuracy of the different

8 conditions between 97.75% and 99.65% (mean 98.64%, for average RTs in each

9 condition see Table S2 in supplementary materials). RTs were initially trimmed to

10 remove responses quicker than 100 ms. RTs more than 2.5 standard deviations from

11 the mean of each participant were then discarded in a non-recursive manner.

12 Discarded trials were fewer than 2% of the total trials.

13   The RT data were initially entered into an analysis of variance (ANOVA) with

14 co-location (correct vs. incorrect), object layout (active-left vs. passive-left), response

15 compatibility (with the active objects vs. the passive objects) and rTMS location (Cz,

16 aIPS and LO) as within-subjects factors. Besides the standard analysis of RT data, we

19

1   were particularly interested in the two contrasts found by S.Xu et al. (2015). They are

2   (a) responses aligned with the passive objects in the correct vs. the incorrect

3   co-location conditions, and (b) responses aligned with the active objects vs. with the

4   passive object in the correct co-location condition. S. Xu et al. (2015) found that

5   responses aligned with the active objects were quicker than those aligned with the

6   passive objects in the correct co-location condition (the advantage effect), and that

7   responses aligned with the passive objects in the correct co-location condition were

8   slower than in the incorrect co-location condition (the inhibition effect).

9   There was a significant main effect of response compatibility, $F(1,21) = 20.23$, $p <$

10     $.001$, $\eta^2 = 0.49$, and a significant main effect of co-location, $F(1,21) = 7.42$, $p = .013$, η^2

11     $= 0.26$, while the main effect of rTMS location was not significant, $p = .87$. There was

12   an interaction between co-location and response compatibility, $F(1,21) = 10.92$, $p =$

13     $.003$, $\eta^2 = 0.34$, an interaction between co-location and stimulation site, $F(2,20) = 5.22$,

14     $p = .013$, $\eta^2 = 0.34$, and a significant four-way interaction (TMS location, co-location,

15   layout and response compatibility), $F(2,20) = 6.44$, $p = .007$, $\eta^2 = 0.39$. None of other

16   main effects or interactions was significant.

17   The four-way interaction pointed toward a distinct impact of TMS at different

18   stimulation sites. To verify our hypotheses we conducted a separate three-way

19   ANOVA for each rTMS location, in order to examine whether TMS alters the pattern of

20   responses differently when applied to contrasting regions of interest (see also Cohen

21   Kadosh, et al., 2007).

3.1. Cz condition

In the Cz condition, the three-way ANOVA with co-location, object layout and response compatibility as within-participants factors revealed that the main effect of layout was significant, $F(1,21) = 6.12$, $p = .022$, $\eta^2 = .23$. Responses were quicker when the active objects were presented on the right side (MD = 3 ms). The main effect of response compatibility was also significant, $F(1,21) = 10.79$, $p = .004$, $\eta^2 = .34$. Responses aligned with the active objects were quicker than those aligned with the passive objects (MD = 4 ms). There was a significant interaction between co-location and response compatibility, $F(1,21) = 5.25$, $p = .032$, $\eta^2 = .20$. None of the other interactions was significant. The planned pairwise contrast revealed that responses aligned with the active objects were quicker than those aligned with the passive objects in the correct co-location condition, MD = 7 ms, $t(21) = 3.82$, $p < .001$. The second planned contrast revealed a significant inhibition effect on responses aligned with the passive objects in the correct co-location condition ($RT_{correct\ co\text{-}location} > RT_{incorrect\ co\text{-}location}$, MD = 3 ms, $t(21) = 1.76$, $p = .047$). Hence, the results in the Cz condition replicated the findings by S. Xu et al. (2015).
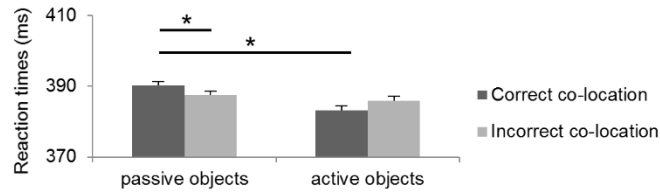
Figure 4. Results of the Cz condition. Responses aligned with the passive objects were slower in the correct co-location condition than in the incorrect co-location condition. Responses aligned with the active objects were quicker than those aligned with the passive objects in the correct co-location condition. The error bars indicate the standard error of each condition following the method proposed by Cousineau (2005).

3.2. aIPS condition

For the aIPS condition, the main effect of response compatibility was significant, $F(1,21) = 9.80$, $p = .005$, $\eta^2 = .32$. Responses aligned with the active objects were quicker than those aligned with the passive objects (MD = 5 ms). There was an interaction between co-location and response compatibility, $F(1,21) = 4.31$, $p = .050$, $\eta^2 = .17$, and a three-way interaction between co-location, response compatibility and layout, $F(1,21) = 10.18$, $p = .004$, $\eta^2 = .33$. None of the other interactions was significant. To break down the significant three-way interaction, we separately analyzed responses in the two object layout conditions.

When the active objects were presented on the left side of the screen, ipsilateral to the stimulation, the main effect of response compatibility was not significant, $p = .16$, nor the main effect of co-location, $p = 0.35$. There was an interaction between co-location and response compatibility, $F(1,21) = 11.65$, $p = .003$, $\eta^2 = .36$. Planned analyses revealed that the advantage of the active objects over the passive objects in the correct co-location condition was significant, MD = 10 ms, $t(21) = 2.25$, $p = .018$, and the inhibitory effect was also significant ($RT_{correct\ co\text{-}location} > RT_{incorrect\ co\text{-}location}$), MD = 9 ms, $t(21) = 3.70$, $p < .001$). In contrast, when the active objects were presented on the

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right side of the screen, contralateral to the stimulation, neither main effects nor the interaction reached significance (the main effect of co-location: $p = 0.10$, the main effect of response compatibility, $p = 0.20$, and their interaction: $p =$s> $0.30)$10. Planned analyses revealed that the advantage of the active objects over the passive objects in the correct co-location condition was not significant, $p = .43$, neither was the inhibitory effect, $p=.070$.

Hence we were able to replicate the advantage of the active objects and the inhibitory effect for the passive objects, as well as the interaction between co-location and response compatibility reported in S. Xu et al.'s (2015) when the passive objects were on the right side and the active objects were on the left side, ipsilateral to the stimulation on the left aIPS, but not when the active objects were presented on the right side, contralateral to the stimulation.
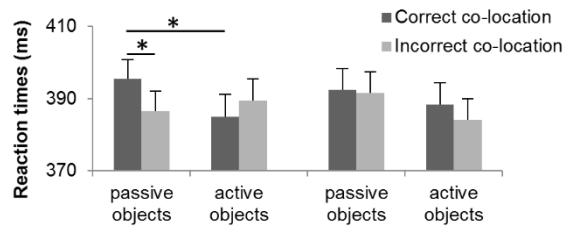
1

Figure 5. Results in the aIPS stimulation condition. When the active objects were

presented ipsilateral to the stimulation, there was an inhibitory effect of implied action

over responses aligned with the passive objects (slower RTs in the correct co-location

condition than in the incorrect co-location condition when the responses were compatible

with the passive objects); there was also an advantage for responses aligned with the

active objects over the passive objects in the correct co-location condition (shorter RTs

when the responses were compatible with the active objects compared with responses

compatible with the passive objects in the correct co-location condition). However, both

effects were absent when the active objects were presented contralateral to the

stimulation. The error bars indicate the standard error of each condition following the

method proposed by Cousineau (2005). The significance of a priori comparisons is

denoted on the figure (a = .05).

3.3. LO stimulation

For the LO stimulation, the main effect of response compatibility was significant,

$F(1,21)= 8.93$, p = .007, η^2 = .30. Responses aligned with the active objects were

quicker than those aligned with the passive objects (MD = 4 ms). The main effect of

co-location was significant, $F(1,21)$ = 12.97, p = .002, η^2 = .38. Responses in the

correct co-location condition were slower than in the incorrect co-location condition

(MD = 4 ms). No other interaction was significant. Because of the pre-defined contrasts

of interest (the advantage effect and the inhibitory effect), we conducted one-tailed

pairwise comparisons between the conditions of interest. The advantage effect was

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significant, $t(21) = 3.01$, MD = 6 ms, $p = .0034$, and so was the inhibitory effect, MD =

6 ms, $t(21) = 3.12$, $p = .0026$ (see Figure 6). In summary, though the interaction

between co-location and response compatibility was not significant, the planned

contrasts showed that the two effects of interest persisted under the LO stimulation

condition.
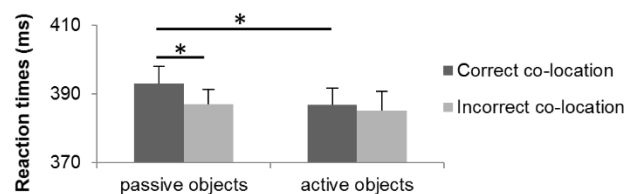
Figure 6. Results of the LO stimulation. Revealed by planned contrasts, there was an

inhibitory effect of implied action over responses aligned with the passive objects (slower

RTs in the correct co-location condition than in the incorrect co-location condition when

the responses were compatible with the passive objects). There was also an advantage

for responses aligned with the active objects over the passive objects in the correct

co-location condition (shorter RTs when the responses were compatible with the active

objects than when they were compatible with the passive objects in the correct

co-location condition). The error bars indicate the standard error of each condition

following the method proposed by Cousineau (2005). The significance of planned

pairwise one-tailed comparisons was denoted on the figure (a = .05).

3.4 Cross-site comparisons

So far the analysis revealed different patterns for each stimulation site. To

examine whether the patterns also differ in comparisons between stimulation sites, we

conducted three cross-site comparisons using a four-way ANOVA with TMS location,

co-location, object layout and response compatibility as within-subject factors.

The comparison between the Cz and the aIPS conditions yielded a significant four-way interaction between TMS location, co-location, object layout and response compatibility, $F(1, 21) = 10.75$, $p = .004$, $\eta^2 = .34$. Similarly, the pairwise comparison between the LO and the aIPS conditions revealed a four-way interaction between TMS location, co-location, object layout and response compatibility, $F(1, 21) = 11.77$, $p = .003$, $\eta^2 = .36$. In contrast, the same analysis on the Cz vs the LO conditions revealed that TMS location does not interact with co-location, object layout and response compatibility ($p = .46$). Hence, the aIPS stimulation affected the response pattern differently compared to the Cz and the LO conditions while the LO stimulation led to a pattern similar to the Cz.

4. Discussion

We investigated the influence of the ventral and the dorsal visual streams on the processing of action-implying object pairs using brain stimulation. As in our previous study (S. Xu et al., 2015), in the baseline condition (the Cz condition) we found two effects of implied actions between objects: (1) responses to the passive objects were inhibited when objects were positioned for interaction relative to when they were not correctly positioned for action. This is consistent with the notion that competition takes place between the affordances offered by the stimuli, and that the affordances of the passive object (incompatible with the action to the object pair) are suppressed by the competition. (2) responses aligned with the active object were faster than responses

aligned with the passive object. The present study further revealed that TMS stimulation to the dorsal stream (aIPS) but not the ventral visual stream (LO) disrupted these effects of implied actions, and that the impact of the aIPS stimulation was modulated by the object layout, since the aIPS stimulation only disrupted the effects when the active objects were presented on the right side, contralateral to the stimulation. In contrast, the evidence of the LO and the ventral stream involvement was not as clear. Note that tTo verify further the unique role of the aIPS we also compared the stimulation data with our data from non-stimulation study (S. Xu, et al., 2015, Experiment 1). Again we found that the response patterns in the aIPS stimulation (but not in the LO stimulation) differed significantly from response pattern without TMS stimulation in S.Xu et al (2015), Experiment 1 (see Supplementary material for detailed analysis). Overall, our results suggest that the aIPS plays an important role in generating the effects of implied actions on response selection with object pairs. Our study provides the first causal evidence for the involvement of the dorsal visual stream in the processing of information related to between-object affordance. In the following we will discuss the detailed implications of these findings.

4.1. The Role of Ventral Stream

In contrast to our evidence for the dorsal stream involvement, the present study did not provide evidence as convincing for a contribution of the ventral pathway to the processing of implied actions between objects. For instance,Admittedly, the interaction between co-location and response compatibility became less apparent in the LO stimulation comparing to the Cz condition and the original findings of S. Xu et al.

(2015). However, the cross-site analysis reported in section 3.4 found no statistical difference between the LO and the Cz conditions but a difference between the LO and the aIPS conditions. In addition, the a-prior analysis of the two effects of interests confirmed the similarity of the response patterns between the LO and the Cz conditions, and their distinction from the aIPS condition. Both results suggested a lack of evidence for a fundamental difference between response patterns in the LO and the Cz conditions, suggesting that at least in our paradigm, the functional involvement of the LO in the processing of implied actions between objects was not convincingly supported as that of the aIPS.

These results seem at odds with the literature pointing towards the involvement of the LOC (for review, see Lingnau & Downing, 2015) and other regions in the ventral visual stream (for review, see Johnson-Frey, 2004) in tool perception and tool use as well as in the perception of implied action between objects (e.g. Kim & Biederman, 2011; Kim, Biederman, & Juan, 2011; Roberts & Humphreys, 2010a). The tasks in these studies required some access to semantic knowledge – depending on action understanding/knowledge retrieval (e.g. Perini, et al., 2014), the functional interpretation of actions (e.g. viewing meaningful tool use vs. non-meaningful tool use, or deciding whether two objects are used together), or object identification/categorization (Kim & Biederman, 2011; Kim, et al., 2011; Roberts & Humphreys, 2010a). In contrast, in the present study the task can be seen as "semantic-free" since it required only decisions about the shape in the center of the screen, not any semantic knowledge of the object pairs on the screen. The Considering the semantic-free nature of our task, the failure to find a TMS effect for the LOC suggests that our effects of implied between-object affordances are not based on semantic knowledge.

However, as admitted in the opening paragraph of this section, though the two a-prior contrasts remained significant in the LO condition and the direct comparison

between the LO and the Cz stimulation was not significant (Sec. 3.4), the present study found no significant interaction between co-location and response compatibility in the LO condition, which is at odds with the Cz condition and S. Xu et al. (2015). The inconsistency between the LO and the Cz conditions calls for caution and prevents the present study from ruling out conclusively a contribution of the LO in the processing of implied action between objects. Further work is needed to provide more direct evidence in this aspect.

4.2   Dorsal contribution to the processing of implied actions

We found that TMS to the aIPS affected the effects of implied between-object actions on responses to paired objects. It eliminated the inhibitory effect on the passive objects and the advantage of the active objects when the active objects were contralateral to the stimulation. This is consistent with the functions of the aIPS in processing single-object affordance, while our results further showed that the aIPS not only contributes to the processing of affordance on a single-object level, but also respond to affordance information embedded in the spatial and functional relations (e.g. whether the co-location was correct for interaction) between objects. Especially, through the usage of TMS the present study provided the first causal evidence from healthy participants for the proposed involvement of affordance-related dorsal-stream processing in the processing of implied between-object affordances.

The aIPS is thought to play a critical role in action-oriented object processing, including online control of object-directed grasping (Binkofski, et al., 1998; Culham, et al., 2003; Frey, et al., 2005; Rice, et al., 2007; Rice, et al., 2006; Tunik, et al., 2005),

1   action observation (Shmuelof & Zohary, 2005), and passive viewing/naming

2   manipulable compared with non-manipulable objects (Chao & Martin, 2000; Chouinard

3   & Goodale, 2012; Mruczek, et al., 2013; Valyear, et al., 2007). Particularly relevant to

4   our results is that the aIPS is reported to be involved in the execution of learned/skillful

5   actions, including complex tool-use behaviors (for review see Johnson-Frey, 2004;

6   Lewis, 2006). It is suggested that the aIPS represents learned knowledge about how to

7   "act with" tools (e.g. Buxbaum, 2001; Johnson-Frey, et al., 2003; Valyear, et al., 2007)

8   as well as information about the hand postures and the critical object structures that

9   are relevant to tool use (Buxbaum, Kyle, Tang, & Detre, 2006; Buxbaum, Sirigu,

10   Schwartz, & Klatzky, 2003; Creem & Proffitt, 2001; Daprati & Sirigu, 2006; Goodale &

11   Humphrey, 1998). For example, an increase in activation for familiar tools was

12   observed relative to other graspable objects in the aIPS and surrounding areas when

13   participants were required to execute tool use actions (e.g. Fridman, et al., 2006;

14   Johnson-Frey, Newman-Norlund, & Grafton, 2005); increased activation in the aIPS

15   has also been found when participants make judgments regarding whether objects are

16   co-located for action (see Bach, Peelen, & Tipper, 2010). This suggests that the aIPS

17   represents information including experience-dependent knowledge of action

18   associations, functions, and potential goals, over and above the mechanical

19   graspability of objects.

20   The established functional role of the aIPS in extracting affordance and

21   representing skilled actions is consistent with S. Xu et al.'s (2015) hypothesis that the

effects of implied between-object actions are based on the direct extraction of

affordances of visually presented objects. The aIPS stimulation might have interfered

with affordance perception of the contralaterally positioned active objects, thus

removing the advantage of the active objects over the passive objects, as well as the

inhibition on the passive objects in the correct co-location condition. Importantly, the

present study suggested that besides single object perception, the aIPS' processing of

the affordance-related information also contributes to the responses to action-related

spatial relation between objects (correct vs. incorrect co-location in our experiments).

A particular effect observed in the aIPS stimulation was that of object layout, i.e.

the TMS stimulation on the left aIPS only affected effects of implied between-object

actions when the active objects were presented contralateral to the aIPS stimulation,

on the right side of the screen. Since we did not find similar layout effect in other

stimulation condition and non-stimulation condition (also with right-handed participants,

S. Xu et al., 2015), it is unlikely that this is an effect of handedness.

Instead, such a layout effect is consistent with the contralateral preference of the

aIPS in affordance-related processing (e.g. Binkofski, et al., 1998; Culham, et al., 2003;

Johnson-Frey, et al., 2005; Shmuelof & Zohary, 2006). supports our claim that aIPS

is involved in processing affordance-related information, probably the affordance of the

active objects, in the perception of implied between-object actions. Previous studies

have found that the left aIPS has a preference to contralateral hand-object interactions

in action observation (Shmuelof & Zohary, 2006), and that the aIPS shows a

1   preference to contralateral acting hands during grasping (Binkofski, et al., 1998;

2   Culham, et al., 2003; Johnson-Frey, et al., 2005). In our paradigm, even though the

3   responses were actually made by the same hand, each object was presented

4   lateralized. Consequently, in our experiment, the aIPS on the left hemisphere might

5   predominantly affect the processing of the contralateral objects. Since the stimulation

6   effect was only apparent when the active objects were presented contralateral to the

7   stimulation, it naturally leads to the conclusion that the aIPS processing of the active

8   objects was critical for the perception of implied between-object actions, and when it

9   was interfered by contralateral aIPS stimulation, the effects vanished, but when the

10   active objects were ipsilateral to the stimulation and was less affected by the left aIPS

11   stimulation, its affordance-related information can still be extracted by the

12   un-stimulated right aIPS and the two effects of implied action preserved. However,

13   admittedly that since we only stimulated the left aIPS (because previous studies

14   suggested a left-lateralized tool-use network), the object contralateral to the aIPS

15   stimulation was always presented on the right side of the screen, and responses

16   aligned with these objects was always made by the middle finger of the right hand of

17   the participants. Nevertheless, it is unlikely that any difference irrelevant to affordance

18   between responses to the left and right sides of the screen or between two response

19   fingers produced this effect, since the same effect was absent in the Cz and the LO

20   stimulation.

1   According to Gibson's ecological approach of visual perception (Gibson, 1979),

2   affordances directly inform actions. However, it is also possible for the aIPS to respond

3   to between-objects affordance via its involvement in attentional orienting. The aIPS is

4   a critical region in top-down attention orienting (Corbetta, Kincade, Ollinger, McAvoy, &

5   Shulman, 2000; Hopfinger, Buonocore, & Mangun, 2000), and has also been shown to

6   contribute to bottom-up attention capture and salience-based selective attention

7   (Corbetta & Shulman, 2011; Geng & Mangun, 2009; Thiel, Zilles, & Fink, 2004). The

8   unilateral lesion or disruption of the aIPS affects the detection and attentional selection

9   of contralaterally presented visual targets (Driver, Blankenburg, Bestmann, & Ruff,

10   2010; Gillebert, et al., 2011; Plow, et al., 2014; Sack, 2010). It is possible that the

11   effects of between-object affordance depended on the aIPS allocating attention to the

12   active objects in object pairs implying actions. For instance, the active object might

13   have higher salience because of its strong affordance, and the aIPS might respond to

14   the implied between-object actions by extracting the unbalanced salience in the pairs

15   of objects or directing attention accordingly, while the perception of affordance per se

16   might have been carried out in a different brain region. This conjecture would fit with

17   data on temporal order judgments, where the active member of an object pair tends to

18   gain 'prior entry' (Roberts & Humphreys, 2010b). Consequently, when the functioning

19   of the aIPS was interfered by TMS stimulation, such attention allocation was affected,

20   and the response pattern diverged from that elicited by between-object affordances.

21   Note that though we acknowledge that the aIPS might contribute to the processing of

22   between-object affordance via its modulation of attention, we maintain that such

1   attentional modulation and the subsequent inhibition and facilitation effects are evoked

2   by the affordance-related features of object pairs, reflecting the impact of affordance

3   processing, and are not produced by factors irrelevant to implied actions between

4   objects, such as size differences and location differences between the active and the

5   passive objects. First, as discussed in a previous paper (S. Xu, et al., 2015), the size

6   and location differences between the active and the passive objects were maintained

7   across the correct and the incorrect co-location conditions. Consequently, if these

8   factors were critical, there should not be the inhibitory effect of implied between-object

9   actions observed in the Cz condition and in S. Xu et al (2015). Also, the previous study

10   (S. Xu et al., 2015) has demonstrated that it is unlikely that the change of orientation of

11   the objects per se, instead of the change of action relation between objects, produced

12   this effect, since changing the orientation of the passive objects in the incorrect

13   co-location condition did not produce the same response pattern observed in our

14   paradigm (i.e. the inhibition of the responses aligned with the unchanged objects in the

15   correct co-location condition), though the size and shape difference between the active

16   and the passive objects were kept constant.

17   Besides attributing the aIPS stimulation effects to its involvement in

18   affordance-related processing, there is yet another explanation. The aIPS stimulation

19   might have affected motor processes in general, e.g. the motor thresholds (e.g. Koch &

20   Rothwell, 2009) of the two responding fingers, instead of affecting processes

21   specifically related to affordances. In other words, the aIPS stimulation may have

1   selectively affected response speed of one finger regardless of the affordance feature

2   of the objects in displays. However, such an affordance-irrelevant interpretation cannot

3   explain all aspects of our results. On one hand, this explanation can accommodate the

4   diminishing of the advantage of the active object over the passive object, when the

5   active objects were presented contralateral to the stimulation, as the responses to the

6   passive object may have been slowed or the responses to the active objects

7   quickened. On the other hand, this argument cannot easily explain the disappearance

8   of the inhibitory effect (the responses to the passive object in the correct co-location vs.

9   in the incorrect co-location), as both conditions, the correct and the incorrect

10   co-location conditions, would have been made by the same finger in that layout

11   condition and therefore would have been similarly affected by the stimulation. Also, the

12   lack of a main effect of TMS stimulation site, i.e. the responses in the aIPS condition

13   were not systematically slower than in other conditions, is inconsistent with such an

14   account.

15   However, we do not rule out the potential contribution of motor preparation. As

16   mentioned earlier, the aIPS is involved in various aspects of motor planning and

17   execution (Binkofski, et al., 1998; Culham, et al., 2003; Frey, et al., 2005; Rice, et al.,

18   2007; Rice, et al., 2006; Tunik, et al., 2005; Tunik, Rice, Hamilton, & Grafton, 2007).

19   Such processes might be the very mechanism via which affordance-based effects

20   were produced by the aIPS stimulation. Future work is needed to identify the exact

21   motor mechanism involved in the extraction of between-object affordance.

1   Nevertheless, the findings of the present study suggest that, whatever the mechanism

2   is, it is linked with the processing of the affordances of paired objects.

3   One potential caveat in interpreting the impact of the aIPS stimulation in the

4   present study was that the present study used a uni-manual instead of bi-manual task.

5   Admittedly, the compatibility effect in a bi-manual task fits better with Gibson's notion

6   of affordance extraction, i.e. the actions afforded by objects being automatically

7   "potentiated" (e.g. Goslin, Dixon, Fischer, Cangelosi, & Ellis, 2012; Handy, Grafton,

8   Shroff, Ketay, & Gazzaniga, 2003; Tucker & Ellis, 1998). However, previous studies

9   have demonstrated that the processing of affordance-related information produces

10   effects of stimuli-response compatibility for uni-manual responses in both single-object

11   scenarios (Cho & Proctor, 2010, 2011) and paired-object scenarios (S. Xu et al., 2015),

12   justifying the usage of the uni-manual task in our study. The stimuli-response

13   compatibility effects for uni-manual responses are interpreted as evidence for an

14   abstract spatial code generated by the corresponding affordances. This code is

15   assumed to represent spatial properties of the afforded actions independent of the

16   specific motor program necessary to execute these actions. For instance, the spatial

17   code would encode left-right location of an object's handle without specifying the

18   relevant reach and grasp movements. Phillips and Ward (2002) were the first to

19   present strong evidence for such an abstract code. They demonstrated that effects of

20   stimuli-response compatibility in single object scenarios occurred irrespective of the

21   response modality (hands crossed or foot response). In our experiments, the observed

effects might have been produced by the compatibility between the automatically generated left-right codes of the implied actions and the left-right codes of the responses (e.g. left finger vs. right finger). Note that in this sense, we use the term affordance in a relative generalized form, which refers to the action-related information from visual stimuli, but does not limit its impact on the potentiation of the specific manual manipulation of the objects. As we have discussed earlier, the effect of the aIPS stimulation might not affect the extraction of affordance-related information per se, but instead the spatial code or attention orienting generated by affordance-related information in the paired-object scenarios. Future studies will have to explore these possibilities further.

Finally, the present study chose a uni-manual task over a bi-manual one also because such a task avoids the confounding impact of handedness or the lateralized motor effect of TMS stimulation. As we explained in section 4.1, object layout would exclusively decide whether it was the active or the passive object that the responses by the right hand, the dominant hand of our right handed participants, would be aligned with. Consequently, if a bi-manual task was used, it would be difficult to exclude the impact of handedness or lateralized motor effect in explaining any interaction involving object layout and response compatibility.

4.3. Distinction between Active and Passive objects

As already discussed in the above section, an interesting aspect of the aIPS stimulation effect here is that performance was modulated by the relative location of the active objects and the stimulation site; the interference from aIPS stimulation was only apparent when the active objects were presented contralateral to the stimulation, when its processing predominantly relied on the affected left aIPS, but not when it was presented ipsilateral to the stimulated aIPS and can be processed by the un-stimulated right aIPS. Our results suggested that the processing of the active objects is critical for the implied between-object actions to affect affordance selection. When the processing of the active objects is disrupted, the effects of the implied actions disappear.

The particular importance of the active objects in generating the effects of implied between-object actions is consistent with the explanation of our previous studies (S. Xu et al., 2015). We suggested that there was suppression of the affordance to the passive object in order to support the preparation of the between-object actions, with the active object affording a more critical role in these actions, compared with the passive objects. By disturbing the processing of the active objects, this suppression in affordance selection disappears. The dominance of the active objects is also in line with previous conclusions drawn from studies looking at the effect of implied between-object actions on object identification, in which "a bias towards the active objects in an action context" was reported (Roberts & Humphreys, 2011b). For

instance, Riddoch et al. (2003) found that in those trials when extinction patients were only able to report one of the objects in the pairs, patients tended to report the active objects when the functionally related object pair was positioned for interaction.

4.43 Bridging objects into pairs by affordances

Going back to the question raised in the Introduction, is it the ventral or the dorsal visual stream that contributes to the perception of action-related sets of objects? The present study suggests that the dorsal visual pathway automatically responds to the spatial relations between objects according to the action implied by their spatial relationship, i.e. the correct or the incorrect co-location for interaction. Previous studies on visual perception of multi-object visual scenes focused more on the representation of the veridical visual features of the objects such as luminance, orientation, texture, size, shape, on the effects of visual redundancy (for review, see Alvarez, 2011), the categorical/semantic relations between objects (e.g. Mizelle & Wheaton, 2010), and the implications for object recognition and identification (Aminoff & Tarr, 2015; Auckland, Cave, & Donnelly, 2007; de Fockert & Wolfenstein, 2009; Hollingworth & Henderson, 1998). Neural activity reported in studies using such tasks has generally involved occipital and temporal areas (e.g. Aminoff & Tarr, 2015; Kim, et al., 2011; Mizelle & Wheaton, 2010), which is not unexpected since the tasks are generally attributed to the ventral visual pathway (for the functional specialty of the ventral visual pathway, see Goodale & Milner, 1992; Milner & Goodale, 2006, 2008; Ungerleider & Mishkin, 1982). There have also been studies specifically looking at how action

relations between objects affect the perception of multiple-object scenes (e.g. Kim & Biederman, 2011; Kim, Biederman, & Juan, 2011; Roberts & Humphreys, 2010a). They reported that the LO was involved during the processing of implied actions between object pairs, which, as we have discussed in section 4.1, might be because most of these studies utilized tasks involving identifying objects (object identification, Kim & Biederman, 2011; object categorization, Kim, et al., 2011; Roberts & Humphreys, 2010a). In contrast, investigations of the contribution of parietal regions/the dorsal visual pathway in the perception of multiple objects has only began relatively recently (e.g. Aminoff & Tarr, 2015; Y. Xu & Chun, 2009), and the work is still largely focused on the potential role of occipital-parietal regions in the representation of the visual features of the objects/scene. This line of studies has added occipitoparietal regions, including the transverse occipital sulcus (Bettencourt & Xu, 2013; Dilks, Julian, Paunov, & Kanwisher, 2013; MacEvoy & Epstein, 2007) and superior and interior intraparietal sulci (for a review, see Y. Xu & Chun, 2009), into the list of regions contributing to the perception of multiple-object scenes.

In addition to this line of research, the present study not only added spatially defined action relations between objects as yet another item in the list of features which are coded during the perception of multiple objects, but also for the first time reported the reliance of this coding on the dorsal visual pathway. This in turn suggests a functional distinction between scene perception for "action" and scene perception for identification or categorization.

More specifically, as discussed in section 4.2, the layout effect in the aIPS condition further suggested that the dorsal processing of the active objects is critical for the implied between-object actions to affect response selection. It seems that the implied actin from the active towards the passive objects bridged the two objects into a pair, and when the processing of the active objects is disrupted, the effects of the implied actions disappear. This finding is consistent with the explanation of our previous studies (S. Xu et al., 2015). We suggested that there was suppression of the affordance to the passive object in order to support the preparation of the between-object actions, with the active object affording a more critical role in these actions, compared with the passive objects. Note that the dominance of the active objects is also in line with previous conclusions drawn from studies looking at the effect of implied between-object actions on object identification, in which "a bias towards the active objects in an action context" was reported (Roberts & Humphreys, 2011b). For instance, Riddoch et al. (2003) found that in those trials when extinction patients were only able to report one of the objects in the pairs, patients tended to report the active objects when the functionally related object pair was positioned for interaction.

4.~~5~~4. The automaticity of the processing of implied action

One striking property of the effects of implied action is the contrast between the automaticity of the effect and the fact that the implied actions are learned. In the present study, all the object pairs involve man-made objects, and the functional actions associated with the active objects are likely learned. However, once they are learned,

not only the procedure and kinematic routine of the action is internalized, the

recognition of these actions seems to be automated as well. We consider that the

reliance on the dorsal pathway for activation of the motor response to the objects might

provide the foundation of this automaticity. The dorsal pathway has been speculated

as less dependent on intentional modulation and visual awareness than the ventral

pathway (Goodale & Westwood, 2004; Norman, 2002; Pisella, et al., 2000; Schindler,

et al., 2004) and capable of carrying out skilled actions automatically. However, the

present study does not address how the skilled tool-use actions are internalized, or the

exact mechanism behind this automaticity. Further investigation is needed in this

aspect.

5. Conclusion

The present study examined the involvement of the ventral and the dorsal visual

streams in the automatic prioritization of active over passive objects in response to

implied between-object actions (S. Xu, et al., 2015). We demonstrated that the aIPS is

crucial for implied between-object actions to affect response selection. We found that

online rTMS to the left aIPS reduced the inhibitory effect on responses aligned with the

passive objects. These reductions only occurred when the active objects were

contralateral to the stimulation. Stimulation of the left LOC did not produce effect as

strong as the aIPS stimulation. The results suggested that the dorsal visual stream and

1 the affordance-based processing it undertakes contribute to the perception of sets of

2 simultaneously presented objects.

3

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7

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