



Registered Report

The contributions of the ventral and the dorsal visual streams to the automatic processing of action relations of familiar and unfamiliar object pairs

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ABSTRACT

Recent studies suggest that action relations between objects affect behavioral and neural responses to action-related object pairs. Existing evidence indicates the involvement of both visual streams in this process. However, uncertainty remains regarding the functional roles of the ventral and the dorsal visual streams, and their interaction in the perception of the action relations between objects. In particular, it is not clear whether the involvement of either stream is dependent on object recognition. The present study aims to dissociate the effect of object familiarity and automatic extraction of action relations by presenting familiar and novel object pairs, which either indicate action relations or not, in a context where the objects and their identification were task-irrelevant. The present study examines the possibility that the activation of the ventral visual stream is dependent on facilitated object recognition exclusively associated with familiar action relations, and tests whether the dorsal visual stream is recruited in the automatic processing of the action relations in paired-object scenarios. With a set of registered analyses, we revealed that both the dorsal and the ventral streams respond to action relations in paired-object scenarios, and the responses were not exclusive to familiar action relations. Registered dynamic causal modeling analysis revealed that the inherent inter-stream connectivity was inhibited by action relations, and further un-registered analysis revealed that there lacks significant inherent effective connectivity between the two streams. These results suggest that both visual streams respond to the experimental manipulation of action relations in paired-object scenarios, but contribute corresponding information to different computations, leading to dissociations between the neural activities of the two streams. These results for the first time suggested a division of labor between the two visual streams in the automatic extraction of action relations in paired-object scenarios. Future study is needed to further explore the context-dependency of the collaboration of the two streams in processing action-related features in multiple-object scenarios.

1. Introduction

Gibson (1979) postulated in his influential ecological approach to vision that humans directly detect action possibilities (also referred to as affordances) from the environment and use these affordances to determine their actions towards objects. There is now substantial evidence that action possibilities are processed in single-object scenarios (e.g. Bub et al., 2008; Grèzes et al., 2003; Grèzes and Decety, 2002; Phillips and Ward, 2002; Riddoch et al., 1998, 2003; Tucker and Ellis, 1998). It has also been reported that potential actions towards objects can influence behavior even though they are irrelevant to the task, suggesting that affordances are extracted automatically (e.g. Ellis and Tucker,

2000; Phillips and Ward, 2002; Tucker and Ellis, 1998). Moreover, neural responses to action possibilities afforded by single objects have been reported in the dorsal visual stream and frontoparietal regions related to motor control, including the intraparietal cortex and the precentral gyrus (Grèzes et al., 2003; Grèzes and Decety, 2002).

According to these findings, affordances are processed in brain regions typically considered part of the dorsal visual pathway, different from the occipitotemporal visual areas associated with object recognition (for reviews, Gauthier and Tarr, 2016; Grill-Spector and Malach, 2004). This dissociation fits with the theoretical frameworks of the functional specialty of the ventral and the dorsal regions in the two visual stream theory (Goodale and Milner, 1992; Milner and Goodale, 2006,

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2008), or sometimes termed as the direct (dorsal) and the indirect (ventral) routes (Riddoch et al., 1989; Yoon et al., 2002). According to such dichotomy, the ventral visual stream is an occipitotemporal network that uses visual information to construct detailed perceptual representations critical for object recognition. The brain regions in this pathway process the invariant structural characteristics as well as the identity and categorical information of objects (Grill-Spector and Malach, 2004; Ungerleider and Mishkin, 1982). In contrast, the dorsal visual stream, or the direct route, projects from the early visual cortex to the parietal lobe and subserves object localization and visually guided action. It captures dynamic spatiotemporal relationships between objects, and, in the spirit of Gibson's affordance theory, extracts possible actions based on their shape and structure (Buccino et al., 2009; Wulff and Humphreys, 2015). This extraction is constrained by information from the indirect ventral route which contributes to the retrieval of semantic and functional knowledge of objects via object identification (Yoon et al., 2002).

The two streams have also been suggested not to be completely independent. Anatomically, there are bi-directional structural projections connecting regions in the human ventral and dorsal visual streams (Takemura et al., 2016; Yeatman et al., 2014). Functionally, the ventral pathway regions have been reported to represent information typically associated with the dorsal visual stream, such as actions towards objects and movement-related object properties (Bracci and Peelen, 2013; Gallivan et al., 2014; Mahon et al., 2007), while the neural activation in the dorsal visual stream regions has also been reported to reflect ventral-stream processing such as viewpoint invariance (e.g. Konen and Kastner, 2008) and object knowledge (e.g. Almeida et al., 2013; Brandt et al., 2014).

Extending this line of research, existing studies suggest that not only the action possibilities associated with single objects can be directly extracted, but also the action relations between objects (e.g. Green and Hummel, 2006; Riddoch et al., 2003; Roberts and Humphreys, 2010a, 2010b, 2011a, 2011b; Xu and Heinke, 2017; Xu et al., 2015; Yoon et al., 2010). These studies presented images of paired objects commonly used together e.g., a hammer and a nail. In such pairs, one object is the active object (the object being used in the action e.g., the hammer in a hammer-nail pair) and the other object the passive one (the object being acted on by the active object e.g., the nail). Humphreys and colleagues (e.g. Roberts and Humphreys, 2010a; Xu et al., 2015; Xu et al., 2017) varied how the pairs were presented on the screen i.e., their co-location, to manipulate the visuospatially defined action relations between objects. A correct co-location resembles a typical interaction between the objects while in an incorrect co-location the spatial relationship between the two objects does not imply an interaction. For instance, a hammer and a nail may imply interaction when the head of the hammer is in the appropriate location and orientation so that it can hit the nail, but not when the head of the hammer points away from the nail. Note that such visuospatially defined action relations may encompass many types of possible interactions, even those not typical/known for the two objects. In a series of studies with such paired objects, Riddoch et al. (2003) reported that the ability to identify both objects improved in patients with extinction when the objects were oriented in correct co-location implying an interaction. For neurologically typical participants, Roberts and Humphreys (2011a, 2011b) reported that correctly co-located object pairs facilitated object identification, compared to the incorrectly co-located pairs, and correctly co-located objects induced a bias towards identifying the active objects relative to the passive objects in each pair (Roberts and Humphreys, 2010b). Xu et al. (2015) also manipulated visuospatial action relations by changing the co-location between objects. They asked participants to make speeded left/right keyboard responses to a target shape in the middle of the screen which appeared together with the object pairs. Hence not only the implied action relationship as in Roberts and Humphreys (2011a, 2011b) but also the objects were task-irrelevant. They found that when the two objects were positioned in the correct co-location, the responses aligned with the affordance of the active objects were quicker compared to those aligned with the passive

objects—a facilitation effect. In addition to this facilitation effect, the responses aligned with the affordance of the passive objects were slower when the two objects were presented in correct co-locations, compared to when they did not depict an interaction. Taken together, these studies indicate that not only action possibilities of single objects (affordances) are extracted automatically, but also the action relations of paired objects.

Although the behavioral evidence suggests the automatic extraction of action relations between objects, the neural mechanism of such direct processing of action relations remains elusive, particularly the exact roles of the ventral and the dorsal visual streams, their interaction, and their dependence on functional knowledge and object familiarity. For instance, our transcranial magnetic stimulation (TMS) study (Xu et al., 2017) found that interfering with the left anterior intraparietal sulcus (aIPS, a critical region of the dorsal visual stream) with TMS reduced the behavioral effects of action relations between objects, but interfering with the left lateral occipital cortex (LO) did not have such an effect. This suggests that the involvement of the dorsal visual stream is critical for the perception of the action relations between objects. However, this study only used familiar object pairs and therefore did not directly address the perception of action relations independent of object recognition. The involvement of the dorsal visual stream independent of object recognition is indirectly supported by a behavioral study. Xu and Heinke (2017) found effects of action relations involving novel objects unknown to the participants, for which the affordance extraction relied on object structures rather than known functions. Given that the dorsal visual stream rather than the ventral visual stream is considered to extract affordances from the structure of objects (Binkofski et al., 1998; Hoeren et al., 2013), this finding, like the TMS study, suggests the functional involvement of the dorsal visual stream rather than the ventral visual stream. The involvement of the dorsal visual stream in the perception of paired-object affordance is also supported by recent functional magnetic resonance imaging (fMRI) evidence. Roux-Sibilon et al. (2018) reported that the dorsal visual stream responded to paired-object affordance when the participants made a decision regarding the typicality of interaction between objects. However, this task always required object recognition, hence it cannot rule out the possibility that the dorsal involvement was a consequence of influence from the indirect route, i.e. object recognition (Kravitz et al., 2011; Yoon et al., 2002). Therefore, there is no direct fMRI evidence for the involvement of the dorsal visual stream in the automatic processing of action relations between objects (i.e., when objects are task-irrelevant), as well as for its reliance on (or independence from) the input from the ventral visual stream.

Evidence of the involvement of the ventral visual stream and its dependence on object familiarity is also unclear. Though the TMS evidence (Xu et al., 2017) did not identify the ventral visual stream as a critical contributor to the processing of action relations, a fMRI study by Roberts and Humphreys (2010a) found that among occipital-temporal object-selective regions, activation in bilateral lateral occipital complex (LOC), a core region of the ventral/indirect stream, increased in the correct co-location condition compared to the incorrect co-location condition. However, this study used familiar action relations and asked participants to explicitly perform object categorization. Also, a recent fMRI study reported contexture- and task-dependent involvement of LOC in the perception of paired-object affordances (Roux-Sibilon et al., 2018). They found that when participants viewed functionally-related pairs of objects and made semantic decisions about the functional context (i.e., whether the two objects were typically found in the kitchen) or the typicality of interaction between the objects (whether the two objects were typically used together), the left LOC responded more strongly to object pairs positioned appropriately for dominant-hand actions in contrast to the horizontally mirrored co-location. However, when the two objects were both familiar but functionally unrelated, the effect existed only when the participants made a decision about the typicality of interaction between the objects, not during the contextual decision. It is worth noting that all these three studies used familiar objects, that is, objects

associated with a particular identity and semantic knowledge. Given that the LOC and the ventral visual stream are known to be primarily involved in object recognition (Grill-Spector and Malach, 2004), it is possible that the increased fMRI activation in the LOC reflected facilitated object recognition, which may be task-dependent as reflected in Roux-Sibilon et al. (2018), instead of reflecting the automatic extraction of action-related information from object pairs. For objects with an established functional association, the co-locations implying actions may be more familiar and thus may facilitate object recognition more readily than the incorrect co-locations. In other words, in perceiving action relations between familiar objects, the ventral visual stream activation may reflect the extraction of other properties such as familiarity, object categories, object function, material and surface properties of objects, etc., rather than visuospatial action relations. Another possibility is that the ventral visual stream receives input from the dorsal visual stream and its activation is a consequence of the processing of visuospatial action relations. This is feasible given the bidirectional connection between the inferior temporal areas of the ventral visual stream and the parietal regions of the dorsal visual stream in macaque monkeys, the dorsal input to the medial temporal lobe, and the recurrent signals from both the ventral and the dorsal pathways integrated in the early visual areas, the common starting point of both visual streams, via strong feedback connections (for reviews, see Kravitz et al., 2013; Milner, 2017). Passive viewing of elongated tool objects (Chen et al., 2018) and the retrieval of action knowledge associated with tool objects (Kleineberg et al., 2018) have been reported to modulate the effective connectivity from the dorsal to the ventral visual stream. Moreover, interference over the parietal cortex, either through neuromodulation or brain lesions, affects object representations within the ventral temporal cortex (Frank E. Garcea et al., 2019; Lee et al., 2019; Ruttorf et al., 2019). These results demonstrated the involvement of the ventral-dorsal interaction in action-related object processing in single object scenarios. In paired-object scenarios, such involvement, if exists, would also be consistent with our previous TMS finding that interfering with the dorsal rather than the ventral visual stream affected paired-object affordance effects (Xu et al., 2017).

Here we want to provide direct fMRI evidence for the involvement of the dorsal visual stream in the automatic extraction of visuospatially defined action relations between objects and to examine its dependence over input from the ventral visual stream. Moreover, we want to examine whether the involvement of the ventral visual stream is the result of object recognition rather than affordance processing or the input from the dorsal visual stream. To do so, the present study examines how action relations of object pairs affect the activation and the effective connectivity of two representative dorsal and ventral visual-stream regions. We reason that if the extraction of action relations relies on the dorsal visual stream, as suggested by previous behavioral and TMS studies (Xu and Heinke, 2017; Xu et al., 2017), a change in activation corresponding to action relations between both familiar and novel objects should be evident in the dorsal visual stream. Instead, if the dorsal visual stream depends on the input from the ventral visual stream to respond to action relations, such dependence would be reflected in a modulatory effect of experimental manipulations on the effective connectivity from the ventral to the dorsal visual stream. Regarding the ventral visual stream, if its involvement is the consequence of facilitated object recognition consequent to the extraction of action relations, it should only respond to the action relations between familiar objects, not to those between novel objects, which cannot be recognized regardless of action relations. In contrast, if the ventral visual stream also processes visuospatial action relations, or its processing is informed by the dorsal visual stream, the ventral visual stream may also respond to the action relations between the novel objects, and in the latter case, the effective connectivity from the dorsal to the ventral visual stream may be modulated by action relations between objects.

In summary, the present study examines the automatic extraction of visuospatially defined action relations of object pairs and intends

(1) to investigate whether the involvement of the ventral visual stream is conditional on object familiarity, (2) to provide direct fMRI evidence for the involvement of the dorsal stream in automatic extraction of action relations and (3) to examine whether and how action relations between objects modulate the effective connectivity between the two visual streams. Specifically, this study manipulates the visuospatial action relations in familiar and novel object pairs, and separately examines the neural correlates of the automatic perception of action relations of familiar and novel objects in a context where the objects were task-irrelevant. We adopted Xu et al. (2015) paradigm to manipulate the visuospatial action relations by orienting the active objects towards or away from the passive objects, to present the objects in co-location suitable for between-object actions or not, which we termed *correct* and *incorrect co-location* conditions respectively. In terms of familiarity, the present study included two types of object pairs. Each familiar object pair consists of two familiar objects which have established functional and action associations, such as a hammer and a nail. In the novel object pairs, following Xu and Heinke (2017), the active objects were constructed by arbitrarily combining action-related structures, i.e. handles, with arbitrary shapes. We reason that the objects and functional knowledge of such object pairs would be constant (absent for active objects and unchanged for the passive objects across co-location conditions) no matter whether the two objects are presented suitable for interaction (the correct co-location condition) or not (the incorrect co-location condition), and the only difference between the two conditions would be the action relations between objects. By examining the changes in activation induced by the manipulation of action relation when the participants view task-irrelevant familiar and novel objects, the present study will examine whether the involvement of either visual stream in the automatic extraction of action relations depends on the familiarity of the objects. In doing so, the present study followed an ROI-based approach and selected ventral and dorsal object-selective cortical regions near the LOC and the aIPS as the ventral and the dorsal ROIs, respectively. As a representative region within human ventral visual stream, LOC, composed of the LO and the posterior fusiform gyrus (pFs), has been reported to be activated in human neuroimaging studies across a range of object perception and recognition tasks (for review, see Grill-Spector et al., 2001), and showed selectivity to tool- and hand- stimuli (for review, see Lingnau and Downing, 2015). The left LOC was also activated by viewing action-related objects in Roberts and Humphreys (2010a). As a representative region within the human dorsal visual stream, the aIPS has been reported to exhibit increased activation in viewing graspable/tool objects versus other objects (Chao and Martin, 2000; Chouinard and Goodale, 2012; Mruczek et al., 2013; Valyear et al., 2007), mediate online control of object-directed grasping (Binkofski et al., 1998; Culham et al., 2003; Frey et al., 2005; Rice et al., 2007; Tunik et al., 2005) and contribute to various tool-use tasks (for review, see Johnson-Frey, 2004; Lewis, 2006). In addition to processing the affordance of a single object and planning simple prehensile actions, the aIPS is also suggested to be involved in representing the goals of actions (Shmuelof and Zohary, 2005), host a short-term context-specific information capacitor for action planning and execution (Tunik et al., 2007), and contribute to spatiomotor and functional judgment in action observation (Bach et al., 2010). Furthermore, TMS over this region affects online grasping control (Cohen et al., 2009) and behavioral responses to visuospatially-defined action relations between object pairs (Xu et al., 2017). This region has been included in various theoretical frameworks regarding tool use, such as the theory of the two action systems (Binkofski and Buxbaum, 2013). Admittedly, the aIPS is not the only dorsal region that contributes to action-related object perception. Alternative regions of interest exist in the left inferior parietal cortex, such as the left supramarginal gyrus (SMG). However, in contrast to visuospatial driven processing, the SMG seems to be more related to functional use of tools such as the administration, imagination, and observation of a specific tool use action; or tasks requiring the tools to be considered in a specific and meaningful functional context (e.g. Buxbaum, 2017; Goldenberg and Spatt, 2009;

Urban and Caruana, 2014; Reynaud et al., 2016). These scenarios are very different from the one considered here, where the task did not require the participants to purposefully process tool use actions or to consider their functional use. Therefore, the present study chose the aIPS as the representative region of the dorsal visual stream, as it is a promising region to illustrate the contribution of the dorsal visual stream to the processing of visuospatially-defined action relations. Considering the functional complexity and heterogeneity of the dorsal visual stream and the inferior parietal cortex (e.g. Binkofski and Buxbaum, 2013), we do not have specific hypotheses regarding the scope and regional dissociation of the dorsal-stream contribution in the perception of action relations. Instead, we will perform an exploratory whole-brain voxel-wise activation analysis to inspect this issue, to identify regions whose activation significantly changes with action relations of the familiar and the novel object pairs, respectively (see Methods for more details), in the hope of providing additional insight to inform future investigation.

In the present study, we will restrict ROI analysis to the left hemisphere. This is because a left-lateralized network of brain regions has been identified in studies reporting increased activation (1) for tools compared to other objects (Chao and Martin, 2000; Chouinard and Goodale, 2012; F. E. Garcea et al., 2016; Kristensen et al., 2016; Bradford Z. Mahon et al., 2013; Mruczek et al., 2013; Valyear et al., 2007) and (2) during viewing, hearing, executing, planning, and pantomiming tool use (Lewis, 2006) compared to control conditions. TMS over the left aIPS has also been reported to affect online grasping control (Cohen et al., 2009), and TMS to the left lateral occipital area (Brodmann's area 37) slows subjects' reactions for object naming (Stewart et al., 2001).

As positive controls, we will first examine whether action relations of familiar object pairs affect neural activation in the dorsal and the ventral ROIs. We expect to replicate the previous findings of activation change in the ventral stream regions in response to the action relations in familiar object pairs (Roberts and Humphreys, 2010a; Roux-Sibilon et al., 2018) and the TMS evidence (Xu et al., 2017) of the dorsal visual stream's involvement in the response to the action relations between familiar objects. Furthermore, we will examine whether an effect of action relations in novel object pairs can be observed in either visual stream. After establishing the effects of action relations in either ROI, we will conduct a dynamic causal modeling (DCM) analysis to examine our speculation regarding the interaction between the two visual streams. DCM analysis fits fMRI data to a set of realistic models of the coupling between neural populations (the nodes) and how that coupling is influenced by experimental manipulation, and estimates model fit using Bayesian statistical methods. The best-fit model (or family of models) is seen as reflecting the effective connectivity between neural populations (Friston et al., 2003). DCM has been used to examine the effective connectivity between the ventral and the dorsal visual streams in action-related object processing in single object scenarios. Recent studies reported the modulation effect of the retrieval of action knowledge associated with tool objects (Kleineberg et al., 2018) and of toolness (as well as a particular type of tools, the elongated tools, Chen et al., 2018) on the effective connectivity between the ventral- and the dorsal-stream cortical areas. The present study intends to use DCM to examine such modulation in paired-object scenarios. We will construct a model space with the dorsal and the ventral ROIs as two nodes, then compare the fit of models specifying a modulatory effect of action relations on the effective connectivity from the dorsal to the ventral ROI, those specifying modulated effective connectivity in the opposite direction, and those specifying neither (See Methods and Supplemental materials for details).

1.1. Main hypotheses of the present study

Regarding Positive controls:

$H0_{pc_ventral}$: The ventral visual stream ROI will not show an increase in activation in response to the correct-co-location condition of

familiar object pairs compared to the incorrect co-location condition.

$H1_{pc_ventral}$: The ventral visual stream ROI will show an increase in activation in response to the correct-co-location condition of familiar object pairs compared to the incorrect co-location condition

$H0_{pc_dorsal}$: The dorsal visual stream ROI will not show an increase in activation in response to the correct-co-location condition of familiar object pairs compared to the incorrect co-location condition.

$H1_{pc_dorsal}$: The dorsal visual stream ROI will show an increase in activation in response to the correct-co-location condition of familiar object pairs compared to the incorrect co-location condition.

The failure to reject either $H0_{pc}$ may indicate a lack of power, probably due to an overestimation of effect size in *a priori* power analysis.

Regarding the ventral visual stream:

$H0_{ventral}$: The ventral visual stream ROI will not show an increase in activation in response to the correct-co-location condition of novel object pairs compared to the incorrect co-location condition.

$H1_{ventral}$: The ventral visual stream ROI will show an increase in activation in response to the correct-co-location condition of novel object pairs compared to the incorrect co-location condition.

The failure to reject $H0_{ventral}$, i.e. the lack of effect of action-relation of the novel object pairs in the ventral visual stream ROI, may indicate that the ventral visual stream does not process action relations directly. In other words, that result suggests that the ventral ROI may be primarily involved in object recognition and the observed change of neural activity in this region may be the byproduct of object recognition.

Regarding the dorsal visual stream:

$H0_{dorsal}$: The dorsal visual stream ROI will not show an increase of activation in response to the correct-co-location condition of novel object pairs compared to the incorrect co-location condition.

$H1_{dorsal}$: The dorsal visual stream ROI will show an increase of activation in response to the correct-co-location condition of novel object pairs compared to the incorrect co-location condition.

The failure to reject $H0_{dorsal}$, i.e. the lack of effect of action-relation of the novel object pairs in the dorsal visual stream ROI, may indicate that the dorsal visual stream is dependent on the recognition of object pairs to process action relation.

Regarding interactions between the two visual streams:

$H0_{-DCM}$: Action relations do not modulate effective connectivity between the dorsal and the ventral ROIs.

$H1_{-DCM_dorsal_to_ventral}$: Action relations modulate effective connectivity from the dorsal to the ventral ROI.

$H1_{-DCM_ventral_to_dorsal}$: Action relations modulate effective connectivity from the ventral to the dorsal ROI.

The failure to reject $H0_{-DCM}$, i.e. the lack of a modulation effect of action relation on the effective connectivity between the two ROIs, may rule out our speculations that the ventral response is informed by the result of the dorsal processing of action relations, and that the dorsal stream is dependent on or under the influence of object recognition in processing action relations. In contrast, its rejection would indicate that the ventral ROI's response to action relations may be affected by the input from the dorsal ROI ($H1_{-DCM_dorsal_to_ventral}$), or that the dorsal ROI's response to action relations is affected by the input from the ventral ROI ($H1_{-DCM_ventral_to_dorsal}$). Note that the testing of these hypotheses follows the Bayesian approach of inferential statistics which is based on the comparison of model evidence instead of *p* statistics, different from the frequentist approach of inferential statistics.

Note that the decision on sample size in this study is based on the effect size estimation from a pilot sample (see Methods for details). This approach, as well as other methods of *a priori* power analysis, may lead to an overestimation of the effect size and underestimation of the required sample size. Therefore, any null result of the present study should be interpreted with caution and the possibility of the lack of power instead of the true “null effect” explained above should be considered.

In the hypothesis-driven analysis, we avoided any direct comparison between the familiar and the novel object pairs. Instead, we separately examined the effect of action relations on each single type of object pairs, which directly address our research question regarding whether a given visual stream is capable of processing visuospatially defined action relations without relying on object recognition. This is also because familiar and novel object pairs inevitably differ in various irrelevant ways (such as the geometry of the object or semantic associations), which may distort the result of the direct comparison. However, given that the effect of co-location was detected in both ROIs, we conducted an exploratory analysis to examine the interaction between visuospatial action relations and the familiarity of object pairs on the activation in the ROI in question, since this may provide additional insight on the conjunctive effect of action relation and object recognition. Also, an exploratory whole-brain voxel-based analysis was conducted to examine the extent of activation under the influence of the action relations of familiar and novel objects. Given that the task requirements and the stimuli of this study differed in some critical aspects from existing studies, we do not have specific hypotheses for these voxel-based analyses.

The significance of the proposed study is based on three aspects. First, it will examine the functional contribution of the two streams in a paradigm in which the objects are completely task-irrelevant. Therefore, this study may tap into the automatic processing of action relations between objects. This will provide new insights into the longstanding discussion regarding the directness of visual perception and its relation to response generation and motor control (Barsalou, 2008; Clark, 1999; Gibson, 1979; Goodale, 2011; Ositurak, 2014; Varela et al., 1992) by extending the extraction of single-object affordances to the processing of between-object relations. Secondly, this study will advance our understanding of the functional roles of the two visual streams in the perception of action relations. It will examine whether the ventral visual stream's involvement in the perception of action relations depends on object recognition and whether the perception of action relations relies on the dorsal visual stream. These results will provide new insights into the functional specialty of the ventral and the dorsal visual streams in the automatic extraction of action relations by dissociating the impact of object recognition and automatic affordance extraction. Thirdly, the present study will potentially shed light on the interaction between the two visual streams in perceiving paired-object scenarios. Linking our TMS study (Xu et al., 2017) with fMRI studies (Roberts and Humphreys, 2010a; Roux-Sibilon et al., 2018), one may speculate that the ventral visual stream's activation change to action relations may result from a dorsal input into the ventral stream. That is, the extraction of action relations in the dorsal visual stream may affect the processing of the ventral visual stream, maybe by introducing additional visual processing of the features of the novel objects. Testing this speculation may extend previous findings that in single-object perception dorsal-stream processing affects the representations of objects (Mahon et al., 2007; Milner, 2017) or object-oriented actions (Gallivan et al., 2013; Singhal et al., 2013) in the ventral visual stream. Furthermore, the functional specificity of the interaction between the ventral and the dorsal pathway is still not clear (Milner, 2017; Willems and Francken, 2012). By separately manipulating visuospatial action relations in familiar and novel object pairs in a task-irrelevant manner, and including a DCM analysis, the present study may provide new insight on the context-dependence of the functional interaction between the two streams.

2. Methods

2.1. Participants

Thirty participants (right-handed neurologically normal volunteers with normal or corrected-to-normal vision) were tested in addition to a pilot sample of six participants. The handedness of the participants was decided before the scanning with a Chinese version of the Edinburgh Handedness Inventory (Oldfield, 1971; Yang et al., 2018), with an above-zero cut-off score for right-handedness. Written informed consent was obtained before the experiment and the participants received money for their time. There lacks effect size information in the paradigm used in the present study, therefore the sample size was decided based on *a priori* power analysis of the pilot sample (see the ‘Determination of sample size’ section). The formal analysis did not include the data from the pilot sample. The full study including the pilot sample was approved by the Institutional Review Board of Beijing Normal University.

The participants were replaced if (1) any contraindication to fMRI studies was detected in the pre-scan screening questionnaire; (2) a below-zero score was received in the Chinese translation of Edinburgh Handedness Inventory; (3) there was excessive head movement (> 3 mm in any direction across the entire scan) during any scanning session; (4) the data collection was incomplete due to any reason; (5) the overall accuracy in the catch trials was less than 60% or the false alarm rate in the experimental trials was more than 5%; (6) the ventral and dorsal ROIs could not be localized by the method described below; (7) the participants deliberately associated co-location with action relations in the novel object pairs (see Procedure for details). In addition, we planned to exclude runs with more than three abrupt movements (> 2 mm). We would replace the data of that participant who was affected more than one run because of this issue. Data collection ended after the targeted sample size is met. In total 9 participants were replaced. Among them four were replaced due to excessive head movement (> 3 mm in any direction across the entire scan), another one was replaced due to excessive movements (> 2 mm) in more than two runs, and another four were replaced due to incomplete data collection. Among the 30 participants included in the formal sample, one run was excluded for two participants because of excessive head movement. In addition, for DCM analysis the data of one run of another participant was excluded because of problematic realignment in concatenating data across runs for DCM analysis.

Pilot sample Six healthy volunteers (three males and three females, mean age 23 years, range: 20 - 28 years) from Beijing Normal University were recruited. Participants gave written informed consent and were paid for their time. The size of the pilot sample was decided *a priori* following Mumford's (2012) recommendation, and participant recruitment stopped when the number of sign-ups met the target sample size. The same exclusion criteria as described for this study were used, except that the handedness of the participants was self-report, and the false alarm rate in the experimental trials was not recorded. No pilot-sample participant was replaced.

2.2. Stimuli

The trials and stimulus presentation were controlled using MatlabR2016B software (The MathWorks Inc., Natick, MA, USA) with Psychtoolbox 3.

The stimuli of the task runs consisted of grayscale line-drawing-style images of object pairs. Each object was presented on a light gray (200, 200, 200 RGB) background, subtending $3^\circ \times 3^\circ$ of the visual angle. The relative sizes of the objects within each object pair matched their relative sizes in real life. Other stimuli included a fixation cross subtending $0.2^\circ \times 0.2^\circ$ of the visual angle and a target stimulus for the catch trials (0, 121, 212 RGB, subtending $0.5^\circ \times 0.5^\circ$ of the visual angle).

The familiar object pairs were a subset of the stimuli used in previous studies investigating the behavioral impact of action relations (Xu et al.,

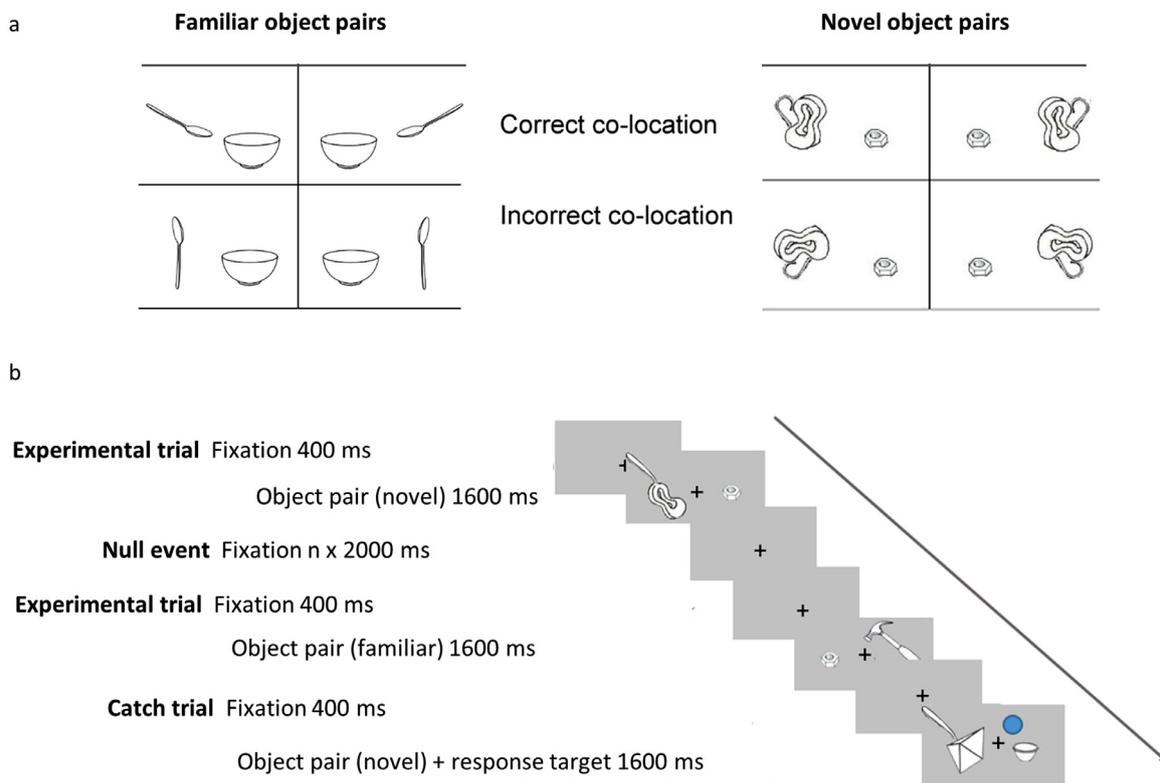


Fig. 1. a. example stimuli of the task run. Left: a familiar object pair. Right: a novel object pair. b. Illustrations of the procedure of the task runs. The first two frames illustrate an experimental trial of novel object pairs in correct co-location, the third frame a number (n) of consecutive null events, the next two frames an experimental trial of familiar objects in the correct co-location, and the last two frames a catch trial.

2015, 2017), consisting of 16 active-passive pairs of objects commonly used together in actions (see Fig. 1 for an example and Supplementary materials for a complete list of the object pairs used). Some stimuli appeared in more than one object pair. For instance, a jug was present in a jug-cup pair and a jug-glass pair. In total, 10 active objects and 8 passive objects were used as stimuli. All the object pairs were presented in the same number of trials in the experiment. However, some objects, both in the familiar and the novel object pairs, appeared in more than one object pair.

The novel object pairs have been previously used in a study investigating the behavioral impact of action relations of novel object pairs (Xu and Heinke, 2017). Each active object combined one of four arbitrary shapes with the handle structure of a spoon, a spatula, a saucepan, or a kettle, resulting in 16 novel active objects. The 16 novel active objects were paired with four passive objects (a nail, a bowl, a tennis ball, and a nut). They were chosen from the passive objects previously used in the paired-object paradigm (Xu et al., 2015). These arbitrary shapes and the passive objects have been chosen because their appearance does not resemble any action-related object pairs commonly seen in daily life (see Fig. 1 and the figure in S2 for example stimuli). This has been confirmed by material evaluation by a separate sample of 12 participants (see Supplementary material of Xu and Heinke, 2017 for the subjective rating).

For both types of object pairs, the correctness of object co-location refers to whether the co-location implies an interaction between the objects or not, and is manipulated by changing the orientation of the active objects. For the familiar object pairs, the co-location is defined as correct when the objects are positioned as if they are interacting in a typical way. An incorrect co-location means that the active object is positioned in an orientation inappropriate to interact with the corresponding passive object. The novel object pairs are assumed to imply an interaction when the handles are on the side of the arbitrary shape opposite to the passive objects, appearing to direct the arbitrary shape towards

the passive objects. Otherwise, the co-location is considered “incorrect” for between-object interaction. The material evaluation reported in previous studies (Supplementary materials of Xu et al., 2015 and Xu and Heinke, 2017) has verified this manipulation of implied action relations between objects. In half of the trials, the active objects were presented on the left side of the screen, while the passive objects appeared on the right side, and the other way around in the rest half.

2.3. Procedure

2.3.1. Data acquisition

MRI scanning was conducted at BNU Imaging Center for Brain Research, Beijing, China, on a Siemens 3T scanner (MAGNETOM Trio, a Tim system) with a 12-channel phased-array head coil. The scanning was separated into two sessions on different days to prevent fatigue. In the first session, each participant underwent 4 task runs and 3 functional localizing runs. In the second session, each participant underwent 4 task runs and 1 structural scan run. One participant underwent the functional localizing runs in session 2 but the structural scan run in session 1 due to technical problem. Functional blood-oxygen-level-dependent (BOLD) images were acquired with a T2*-weighted gradient-echo, echo-planar-imaging (GRE-EPI) sequence (TR = 2 s, echo time = 30 ms, flip angle = 90°, in-plane resolution = 3.1 × 3.1 mm). Whole-brain coverage for the functional data was obtained using images of 33 contiguous interleaved slices. Structural T1-weighted images were acquired with a 3D magnetization-prepared rapid acquisition gradient echo (MP-RAGE) sequence (TR/TE/T1 = 2530/3.39/1100 ms, flip angle = 7°, matrix = 256 × 256) for spatial normalization and anatomical localization of the functional activations. The participants wore earplugs to attenuate the impact of scanner noise, and head motion was restrained with a foam pillow and extendable padded head clamps. All the stimuli were projected onto a screen at the back of the scanner and were viewed from approximately 110 cm via a mirror placed on the head coil.

2.3.2. Localizer paradigm

A dynamic localizer task was used to define the ROIs. Each of the three dynamic localizer runs lasted 198 s, each combining two block sets. An 18-s rest block was added at the beginning and the end of the run, and between the two block sets. Each block set consisted of one 18-s block for each of four stimulus categories (i.e., faces, scenes, objects, and scrambled objects). The blocks consisted of six 3-s color movie clips showing different stimuli of the same category, randomly drawn from a pool of 60 clips. The scene stimuli were mostly views of rural areas from the window of a slow-moving car or views of moving through canyons or tunnels. The object stimuli were mostly slowly moving toys with minimum suggestion of animacy or ongoing human manipulation (for more details, see Pitcher et al., 2011). The order of stimulus category blocks in each run was palindromic and randomized across runs. Participants were instructed to passively view movie clips. For this study, we defined ROIs by the contrast between objects and scenes (see also Roberts and Humphreys, 2010a; Roux-Sibilon et al., 2018).

2.3.3. Task runs

The present study followed a rapid Event-related design. Each task run consisted of 128 experimental trials, 16 catch trials, and 32 null event trials, lasting for 6 min 10 s. The participants were instructed to make an index-finger response as quickly and accurately as possible when they see a blue target (i.e. the catch trials). The catch trials were included in the design to ensure the participants' attentiveness, and were excluded from fMRI analysis. The participants used their dominant right hand to respond.

The 128 experimental trials were evenly divided into four conditions (co-location: correct versus incorrect; object familiarity: familiar versus novel). On each experimental trial participants viewed a fixation cross for 400 ms, followed by a 1600-ms presentation of a pair of objects while the fixation remains on the center of the screen. No response was required in the experimental trials, and the participants were instructed before the scanning session to keep looking at the fixation cross but pay attention to the screen. The catch trials were randomly assigned to the four conditions. Each catch trial also started with a 400 ms interstimulus interval (ISI) with the fixation cross presented, but differed from the experiment trials in that a blue target would appear at the same time as the object pairs at a random location within a $6^\circ \times 3^\circ$ area centered on the screen, and might partially obscure the objects in some catch trials. The presentation of object pairs and target stimuli lasted for 1600 ms regardless of when the participants respond. Each null event trial, where only the fixation cross was presented on the center of the screen, lasted 2 s (400 ms ISI followed by 1600 ms null events, matching the length of the experimental trials), and several null event trials were presented consecutively. The order of the trials and null events was optimized using optseq2 (Dale, 1999). The pilot data for this study was collected using the same methods as described above.

After the completion of the last scanning session, the participants were invited to fill in a post-scan questionnaire to report on whether they noticed the difference between experimental conditions during the scanning. They were asked to describe what they noticed or speculated, particularly about the novel object pairs, and how frequently they deliberately examined the noticed/speculated features. The questions were printed in Chinese and participants were required to write the answers (see Supplemental materials for the English translation of the questionnaire).

Participants who differentiate co-location conditions by whether they are "correct/appropriate/functional" or "right for action/interaction", or by any other expression indicating an association of co-location and action relations in novel object pair conditions AND indicate deliberately examining this association during the scanning would be questioned further by an experimenter, to confirm the frequency they examined this association (in contrast to other differences they may have noticed) during the scanning. The experimenter was trained beforehand to recognize such associations.

After the scanning, a graduate researcher trained in psychology or cognitive neuroscience was invited to check the participants' responses, to re-evaluate whether a participant's response to question 3 indicates associating co-location with action relations in novel object pair conditions. No participant was judged by both the experimenter and the re-evaluator to have noticed/speculated the association between co-location and action relations in novel object pairs AND selected option 1–4 in question 4 (1: in every trial, 2: more than half, 3 half of the trials or 4: less than half of the trials), therefore no participant was replaced because of this issue. Besides, as pre-registered, the last run of those who reported such association and select option 5 in question 4 was to be removed from the analysis, and no participant fulfilled this condition. All the participants received consentaneous judgment that they did not indicate regular deliberate examination of this association (by selecting options 1–4 in the corresponding question). We did not replace participants who differentiate the co-location conditions of familiar object pairs by their appropriateness for action in the main results. This is because the typical layout of familiar objects may be part of manipulation knowledge or experience of these objects. For instance, a participant may recognize that the paired-object scenarios (with familiar objects) in the incorrect co-location condition as being visually unfamiliar and therefore 'incorrect', without considering whether the visuospatial relationship between the two objects is appropriate from the perspective of a between-object interaction. Therefore, a reported association between action relation of familiar object pairs and the co-location manipulation in the questionnaire may not necessarily be the result of the processing of visuospatial action relations as such. Instead, it may suggest that the processing of action relations can be driven by knowledge aspects of object perception (e.g. the familiarity with a given visual scene). No participant associated co-location of familiar object pairs with action relations and deliberately examined this feature.

2.4. Data analysis

2.4.1. Behavioral data

The overall hit rate of the catch trials, the hit rate and reaction time (RT) of each condition in the catch trials, and the false alarm rate in the experimental trials were calculated, but inferential statistics of behavioral data were not reported since we did not have hypotheses regarding behavioral responses in the catch trials.

2.4.2. fMRI data

Data preprocessing was performed using the DPABI software (Yan et al., 2016, <http://rfmri.org/dpabi>). The main preprocessing procedure was as follows: (1) transformation of DICOM files into NIFTI images; (2) slice timing; (3) head motion correction; (4) co-registration of the high-resolution T1-weighted structural images to the functional images; (5) segmentation of the data; (6) spatial normalization to the standard Montreal Neurological Institute (MNI) space, and resampling to $3 \times 3 \times 3$ mm isotropic voxels; (6) smoothing with a 4 mm full-width-half-maximum Gaussian kernel.

The task-run data was modeled at the individual level with regressors for each condition (familiar objects in correct co-location, familiar objects in incorrect co-location, novel object in correct co-location, and novel objects in incorrect co-location), each in two different object layouts (whether the active objects were presented on the left or the right side of the fixation), using the SPM12 software (Wellcome Department of Imaging Neuroscience, London; www.fil.ion.ucl.ac.uk/spm). Additional regressors were added for the null events, and the catch trial. The presentation of the fixation cross was not modeled since it was constantly presented during the experiment. The regressors were convolved with the canonical haemodynamic response function (HRF). A 1/128 Hz high-pass filter was applied to remove low-frequency noise, using an AR(1) model to account for serial correlations. The pilot data were pre-processed using the same approach.

ROI analysis: activation We localized each participant's ROIs based on their own data from the dynamic localizer runs. The localizer data were modeled at the individual level using SPM12 (Wellcome Department of Imaging Neuroscience, London; www.fil.ion.ucl.ac.uk/spm) with regressors for each stimuli category (faces, objects, scenes, scrambled objects) convolved with the canonical haemodynamic response function (HRF). A 1/128 Hz high-pass filter was applied to remove low-frequency noise, using an AR(1) model to account for serial correlations. We identified subject-specific regions that were more active when participants viewed objects than when they viewed scenes (objects > scenes, $p < 0.005$ uncorrected, extent greater than 5 suprathreshold voxels). We then extracted the peak coordinates of the subject-specific object-processing clusters (or the local maxima more than 4 mm apart from each other when occipitotemporal cortex and posterior parietal cortex were included in a single cluster) and calculated the Euclidean distance between the peak coordinates to the corresponding group-average coordinates of the TMS stimulation sites (the aIPS, [-37, -42, 44] and the LO, [-44, -66, -11]) reported in Xu et al. (2017). Among the peak voxels (1) within 40 mm of the corresponding group average site AND (2) within an anatomical mask of the occipitotemporal cortex (based on the AAL templates of the left inferior and the left middle occipital gyri, and the left inferior and middle temporal gyri with one-voxel 3D dilation) for the ventral ROI, or within an anatomical mask of the posterior parietal cortex (based on the AAL templates of left inferior parietal, superior parietal and postcentral gyrus with one-voxel 3D dilation) for the dorsal ROI, we identified the one with the highest magnitude in the object-selective contrast to be the center of the ventral or the dorsal ROI. The anatomical masks were derived from WFU Pick-atlas (<http://www.fmri.wfubmc.edu>; Advanced Neuroscience Imaging Research Core, Wake Forest University, Winston-Salem, NC, USA) with one-voxel 3D dilation. We then defined the subjective-specific dorsal and ventral ROIs by creating a 5-mm radius spherical ROI centered on respective subject-specific peak coordinates using the Marsbar toolbox (<http://marsbar.sourceforge.net/>).

We used the MarsBar toolbox to extract the parameter estimates from the first-level analysis of task run data from each ROI for each participant and each condition. A paired-sample t -test was calculated based on the average parameter estimates of corresponding conditions within each subject-specific ROI. Two contrasts of interest were examined: (1) The contrast between *familiar objects in correct co-location* and *familiar objects in incorrect co-location* which reflects the effect of action relations between familiar objects. (2) The contrast between *novel objects in correct co-location* and *novel objects in incorrect co-location* which reflects the effect of action relations between novel objects. Given that an elevation of LOC activation in response to action relations in familiar object pairs (Roberts and Humphreys, 2010a) and the interference effect on action-relation processing when aIPS receives online TMS stimulation (Xu et al., 2017) has been previously reported, we took the one-tailed paired-sample t -test of the contrasts of familiar-object-pair action relations (*familiar objects in correct co-location* > *familiar objects in incorrect co-location*) of each ROI as two positive controls for this study. Bonferroni correction was applied in examining the positive control contrast with the corrected significance level being 0.05. Except these two positive controls, all the statistical tests in this study were two-tailed. Bonferroni correction was also applied in examining the contrast between *novel objects in correct co-location* and *novel objects in incorrect co-location* since both ROIs were analyzed for each contrast, with the corrected significance level being 0.05. The same ROI analysis was conducted for the pilot sample.

ROI analysis: dynamic causal modeling This analysis was conducted using Bayesian model comparison analysis based on the dynamic causal modeling module of SPM12 (Friston et al., 2003; Stephan et al., 2010). It consisted of the following steps.

A. *Construction of the model space.* We constructed a model space using the dorsal and the ventral ROIs as two nodes, and included the

four main conditions (familiar object pairs in the correct co-location, familiar object pairs in the incorrect co-location condition, novel object pairs in the correct co-location condition, and novel object pairs in the incorrect co-location condition) as potential input and modulation factors. For the activation change associated with action relations of the familiar object pairs in each ROI, we considered 5 possibilities: (1) no change; (2) by local processing in the form of differentiated activation locked with co-location of familiar object pairs; (3) by input ONLY, i.e., by receiving differential input from the other ROI modulated by the co-location of familiar objects; (4) by local response AND input; and (5) by selectivity to familiar objects regardless of co-location AND input modulated by the co-location of familiar object pairs from the other ROI. For each ROI's response to the action relations between novel object pairs, we considered the counterpart possibilities except that the fifth situation was changed into selectivity to novelty AND (co-location dependent) input from the other ROI. See Table S2 for more details of model operationalization. To simplify the analysis and stay close to our hypotheses, we did not include models with loops (action relations of the same kind of objects affecting the effective connectivity in both directions), models with connections not affected by any factor, models predicting selectivity to both familiarity and novelty in the same ROI, and models predicting one ROI to locally process action relations of both types of object pairs but only inform the other ROI of one type. Also based on the known functionality of the dorsal and the ventral visual streams we excluded models that predict the ventral ROI selectively processes or informs the dorsal ROI action relations between novel but not familiar object pairs, and models that predict the ventral ROI to selectively respond to object novelty regardless of co-location. Based on previous TMS evidence (Xu et al., 2017), we also excluded models that predict the dorsal ROI to exclusively rely on input or selectivity to familiarity to respond to action relations of the familiar object pairs. These criteria led to a pool of 36 models.

B. *Restricting the model space with observed activation results.* In the resultant models, we only kept those predicting activation changes in a given ROI consistent with the results of ROI-based activation analysis. In the case of the present study, we observed activation changes associated with action relations of both novel and familiar object pairs in the ventral ROI, as well as in the dorsal ROI. Therefore, we accordingly excluded models that predict no activation change of either ROI associated with these manipulations (See Fig. 2 for the illustration of each model in the restricted model space).

C. *Bayesian model comparison.* Based on the model pool conditional to the activation analysis, we estimated each model in the restricted model space and compared the respective model exceedance probabilities. The time series subjected to estimation of effective connectivity were derived from the task-run data based on the same design matrix of activation analysis, and a group-level random-effects Bayesian model comparison analysis was conducted. We reported the best fit model and the probability of equal model frequencies (BOR) of the comparison.

D. *Family-level inference.* The tested models were then be divided into families according to whether they specify any modulation effect of action relations on (1) the effective connectivity from the dorsal to the ventral ROI, (2) the effective connectivity from the ventral to the dorsal ROI, and (3) neither. We compared the family exceedance probabilities, reported the winning family, and examined the acceptance or refusal of the corresponding hypotheses.

Pre-specified exploratory analyses To comprehensively illustrate our data, since we detected the effect of co-location in both kinds of object pairs in both ROIs, we conducted an ROI-based analysis of the interaction between action relation and object familiarity, as part of pre-specified exploratory analyses. The result of this analysis should be evaluated with caution given the stimuli difference between two types

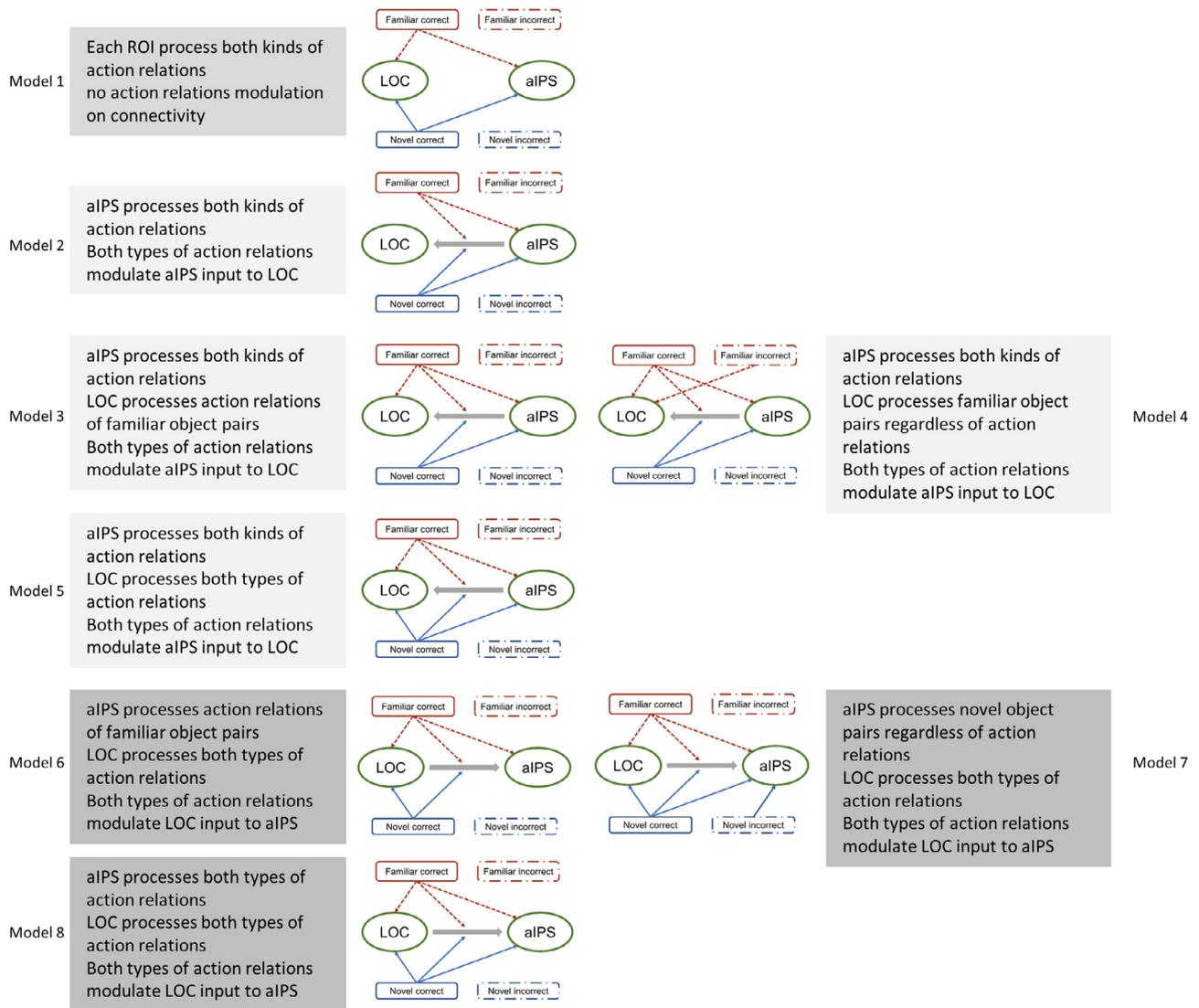


Fig. 2. Model summary of the restricted model pool.

of object pairs (such as the geometry of the object or semantic associations). The first-level estimate of ROI-based activation in the four main conditions was submitted into a repeated measure ANOVA with familiarity (familiar vs novel) and action relation (correct vs incorrect) as within-subject factors.

As a conditional follow-up step in the DCM analysis, if the BMS analysis indicated superior fit for model(s) with a modulatory effect of action relations on effective connectivity between ROIs, to illustrate the inter-participant consistency of this modulatory effect, individual parameter estimations of the modulatory effect from the familiar-correct condition and that from the novel-correct condition in the winning model were subjected to one-sample *t*-test (two-tailed), to examine whether each modulatory effect modeled in the winning model consistently deviates from zero across participants. Bonferroni correction was applied with the corrected significance level being 0.05.

In addition to ROI analysis, we also conducted a whole-brain voxel-based analysis to identify regions whose activation significantly changes with action relations of the familiar and the novel object pairs, respectively. We conducted second-level voxel-based analysis for these contrasts using SPM12 within a gray matter mask. The mask would be derived from the bilateral gray matter atlas of WFU Pickatlas with one-voxel 3D dilation. The analyses were performed using one-sample *t*-tests on contrast images obtained from each participant for each con-

trast of interest. Clusters were reported with a voxel-level threshold of $p=0.001$ uncorrected, and a cluster-extent threshold of $p=0.05$ corrected for family-wise error at the cluster level, using the random field theory approach implemented in SPM12.

We also tested these proposed voxel-wise analyses in the pilot data (See Supplemental materials S4), albeit with a more liberal threshold due to the exploratory nature of this analysis with a small sample size. Note that, being a common approach of thresholding, the cluster-based approach has been found to run the risk of inflating type I errors (Eklund et al., 2016; But see Flandin and Friston, 2019), and thus the estimation of spatial extent should be interpreted with extra caution.

For the results of this voxel-wise analysis, the data inspection was planned to focus on describing the scope and regional dissociation of the dorsal visual stream in the processing of action relations of either type of object pairs, i.e., the spatial scope of parietal regions responding to action relations of familiar and novel object pairs. The scope of the neural response to action relations of either type of object pairs was examined against the structural atlas of regions reported to be involved in either affordance processing or skilled tool use (the left inferior parietal cortex, the left superior parietal cortex, the left angular gyrus, and the left supramarginal gyrus in Automated Anatomical Labeling, AAL). We reported the location and the dice coefficient of the overlaps between the activated cluster and the corresponding AAL labels. In addition, we

examined the difference in the scopes of the co-location effects of familiar and novel object pairs. The location of the overlap and the dice coefficient of the two thresholded activation maps in the above-mentioned AAL masks were reported.

Unregistered follow-up analyses Besides the registered analyses, to fully understand the findings of the registered analysis, for the formal sample we conducted two sets of unregistered follow-up analyses. First, to further explore the dynamics predicted by the winning model (negative modulation of the ventral to the dorsal connectivity through familiar-correct condition), we analyzed the parameters for all the direct inputs and inherent connectivity specified by this model i.e., that from the familiar-correct as well as the novel-correct conditions on both the ventral and the dorsal ROIs and from the novel-incorrect condition on the dorsal ROI, and the inherent effective connectivity from the ventral to the dorsal ROI. One-sample *t*-tests (two-tailed) were conducted to examine whether each direct effect modeled in the winning model consistently deviates from zero across participants. Bonferroni correction was applied with the corrected significance level being 0.05. Also, since the relative amplitude between the direct impacts from the novel-correct and the novel-incorrect conditions to the same ROI reflects whether that ROI responds to action relations between novel object pairs or to novelty per se, we compared the direct impacts from the novel-correct and the novel-incorrect conditions to the dorsal ROI in the winning model. Paired-sample *t*-tests (two-tailed) were conducted with the significance level being 0.05.

Further, after noticing that the inherent effective connectivity turned out to be not significant in the winning model (model 7; see results for details), we considered the possibility that the present study did not produce strong evidence of the direction of the inherent connectivity between the two ROIs. To test this possibility we added a new model into the original model pool with its structure the same as the winning model but replacing the inherent connectivity with one of an opposite direction, from the dorsal to the ventral ROI, to form an expanded model pool (Model 9; Fig. 3). We applied the same DCM-based model comparison and parameter analysis to the extended model pool with this additional model.

2.5. Determination of sample size

To determine the size of the formal sample, we conducted *a priori* power analysis by submitting the observed effect size in the pilot sample to *G*power* 3 (Faul et al., 2007) to estimate the required sample size to achieve a power of 0.9 and an alpha level of 0.05 (Bonferroni corrected) for a paired-sample *t*-test. One-tailed tests were used for the positive controls while the rest of the tests were two-tailed.

To ensure that we are able to replicate the effect of action relations between familiar objects reported in previous studies (Roberts and Humphreys, 2010a; Roux-Sibilon et al., 2018; Xu et al., 2017), we first estimated the required sample size for the positive control analyses. To do so, we examined the action relation effect of familiar object pairs in the ventral and the dorsal ROIs, separately. In the ventral ROI, there was a trend towards higher activation levels in the *familiar objects in correct co-location* condition compared to the *familiar objects in incorrect co-location* condition. The group-level contrast was not significant ($p = 0.10$), with an observed effect size $d_z = 0.62$. The *a priori* power analysis indicated a sample size of 30 participants. For the dorsal ROI, there was a trend towards higher activation levels in the *familiar objects in correct co-location* condition compared to the *familiar objects in incorrect co-location* condition. The group-level contrast was significant ($p = 0.04$), with an observed effect size $d_z = 0.91$. A *a priori* power analysis revealed that, with the given effect size, a sample size of 15 subjects will reach the required power of 0.9. Based on these results, a sample size of 30 was chosen for the formal sample.

We also conducted an ROI analysis of the effect of action relations between novel object pairs in the ventral and the dorsal ROIs separately and conducted an *a priori* power analysis. The results indicated that the

activation levels in the dorsal ROI tended to be higher in the *novel objects in correct co-location* condition compared to the *novel objects in incorrect co-location* condition. The group-level contrast was not significant ($p_{\text{unc}} = 0.06$) with an observed effect size $d_z = 0.99$. The *a priori* power analysis suggested that 16 participants are needed. The same contrast was also not significant in the ventral ROI, with a trend towards higher activation in the *novel objects in correct co-location* condition compared to the *novel objects in incorrect co-location* condition ($p_{\text{unc}} = 0.11$) with an observed effect size $d_z = 0.79$. The *a priori* power analysis estimated that a sample of 23 participants is needed. With the chosen sample size of 30, we should have adequate power in examining these effects in the formal sample.

3. Results

Behavioral responses in the catch trials Participants were highly accurate, with an average hit rate in the catch trials of 98.0% (SD = 3.7%). The hit rate and the RTs in the catch trials were summarized according to the types of object pairs in each catch trial (Fig. 4).

Localization of the ROIs The ROIs were localized by the approach detailed in the Methods, except using SPM8 instead of SPM12. We were able to identify both ROIs in all the pilot participants. The average MNI coordinates of the ventral ROI were $[-49.4, -68.5, -2]$, the average Euclidean distance between individual ROIs and the group average LOC in a previous TMS study on paired object affordance (Xu et al., 2017) was 10.8 mm. The average MNI coordinates of the dorsal ROI were $[-34.9, -51.2, 49.8]$, the average Euclidean distance between individual ROIs and the group average aIPS in a previous TMS study on paired object affordance (Xu et al., 2017) was 11.1 mm.

To ensure that we have achieved enough power with the present sample size, we first examined the action relation effect of familiar object pairs in the ventral and the dorsal ROIs, separately (Fig. 5a), as the positive controls. In the ventral ROI, there was a significant effect of action relation in familiar object pairs, with higher activation levels in the *familiar objects in correct co-location* condition compared to the *familiar objects in incorrect co-location* condition, $t(29) = 6.66$, $p < 0.001$, $d_z = 1.22$, MD = 2.10. For the dorsal ROI, the effect of action relation in familiar object pairs was also significant, with higher activation levels in the *familiar objects in correct co-location* condition compared to the *familiar objects in incorrect co-location* condition, $t(29) = 4.67$, $p < 0.001$, $d_z = 0.853$, MD = 2.17.

With the positive control checked, we proceeded to examine the ROI-wise effect of action relations in novel object pairs in the ventral and the dorsal ROIs separately (Fig. 5). The activation levels in the dorsal ROI was higher in the *novel objects in correct co-location* condition compared to the *novel objects in incorrect co-location* condition, $t(29) = 4.73$, $p < 0.001$, $d_z = 0.863$, MD = 2.07. The same pattern was also observed in the ventral ROI, $t(29) = 6.55$, $p < 0.001$, $d_z = 1.19$, MD = 1.69. As part of the pre-specified exploratory analysis, we examined the interaction of action relation and object familiarity in each ROI with a repeated measure ANOVA with familiarity (familiar vs novel) and action relations (correct vs incorrect) as within-subject factors. In both ROIs, the main effects of action relations were significant ($ps < 0.001$), while the main effects of familiarity and the interaction between the two factors were significant in neither ROI ($ps > 0.05$).

DCM analysis Within the model space specified in the Methods section, we made further restrictions and excluded models that predict no activation change associated with either kind of action relations from either ROI. This left us with 8 models (see Fig. 2). Bayesian model comparison was conducted on these models using the dynamic causal modeling module of SPM12.

The results favored model 7, with the model exceedance probability = 0.65 (Fig. 6a), the probability of equal model frequencies = 0.01. Model 7 predicted (1) the activation in the ventral ROI to change with action relation manipulation for both types, familiar and novel, of object pairs, (2) the dorsal ROI to process object novelty (responding to

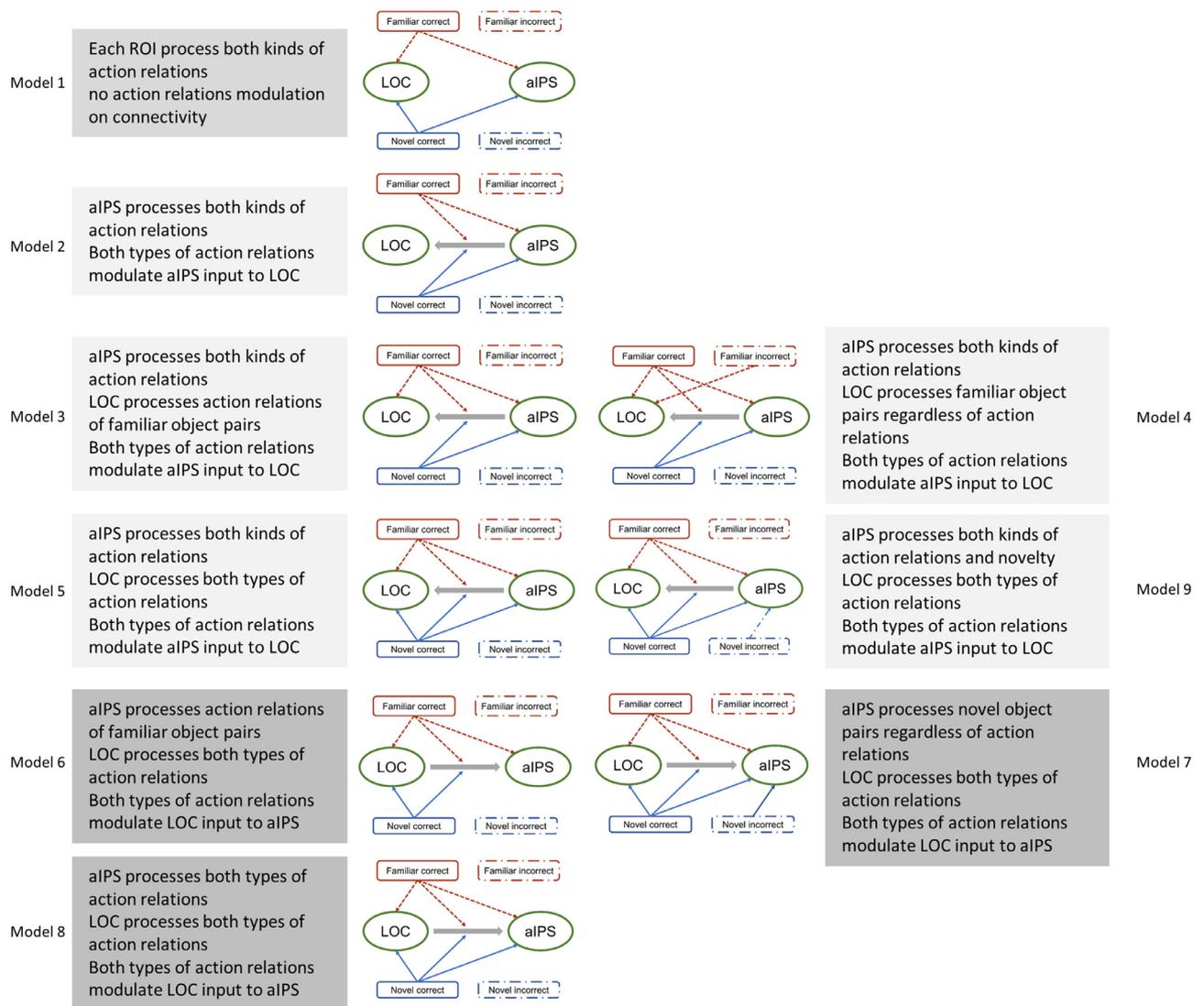


Fig. 3. The expanded model pool. Model 9 was added, with a structure same to Model 7 but specifying an inherent connectivity from the dorsal to the ventral ROI.

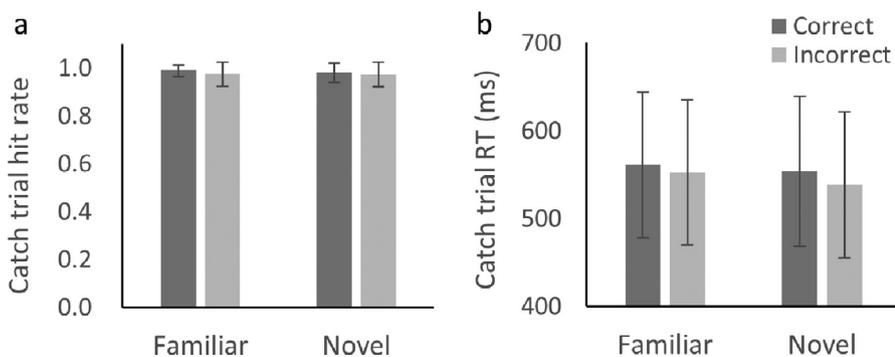


Fig. 4. Hit rate (a) and RTs (b) in catch trials. The error bars denoted the standard errors.

novel objects regardless of co-location) and the action relation of familiar objects, (3) there was inherent connectivity from the ventral to the dorsal ROI, and (4) both types of action relation modulate the inherent connectivity from the ventral to the dorsal ROI.

To further examine the hypothesis regarding the interaction between the dorsal and the ventral visual streams, we divided the 8 models into three families. Four of them predicted effective connectivity from the dorsal to the ventral ROI. The second family (including the winning one) predicted effective connectivity from the ventral to the dorsal ROI.

The third family of one model predicted no connectivity in either direction. A family-level inference was conducted and the family exceedance probability of each family was calculated. The results indicated that the second family fitted the data best (Fig. 6b), suggesting effective connectivity from the ventral to the dorsal ROI.

The best-fit model identified in the BMS analysis predicted modulatory effects of familiar as well as novel object pairs in the correct co-location condition on the effective connectivity from the ventral to the dorsal ROI. As a pre-planned follow-up analysis, we con-

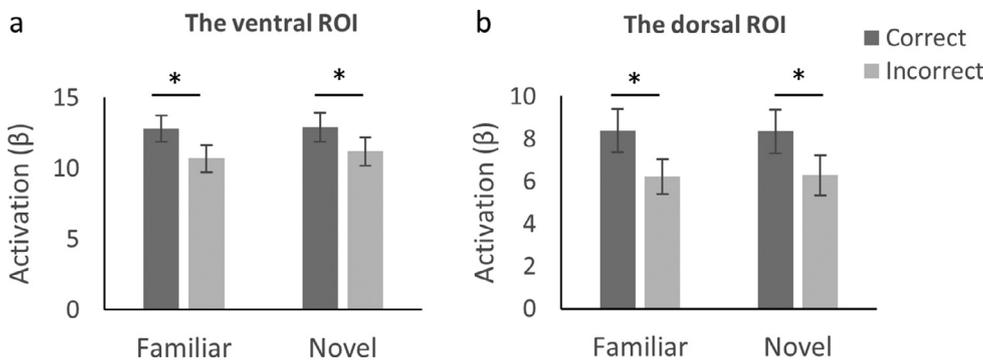


Fig. 5. The ROI-wise effect of action relations in the familiar and novel object pairs. The asterisks denote statistical significance ($p < 0.05$, Bonferroni corrected).

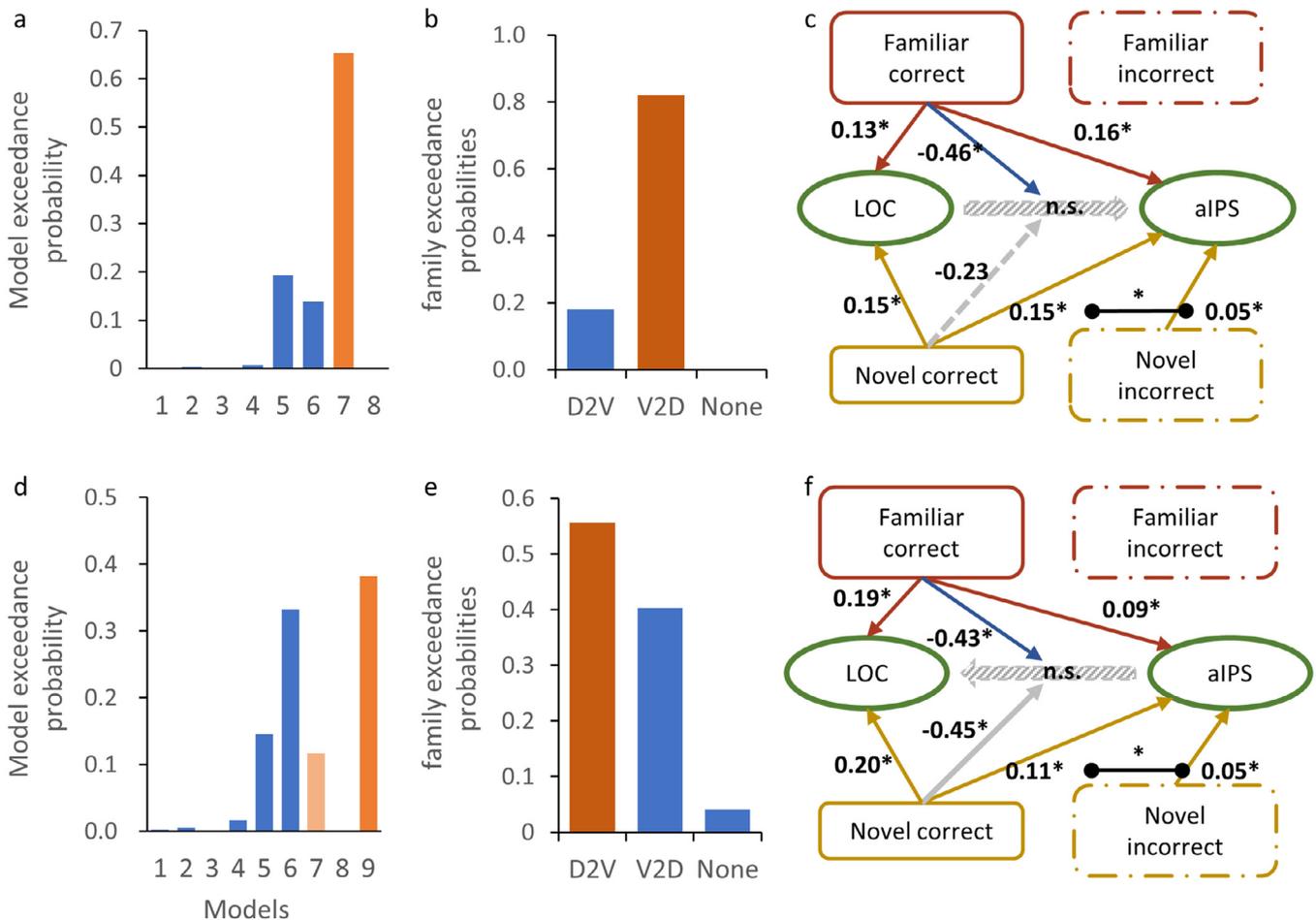


Fig. 6. a. Exceedance Probability of each model in the original model pool. Model 7 is the winning model. b. Family exceedance probability of each family. The ventral-to-dorsal family emerged as the winning family. c. Parameter estimations of the winning model. The solid arrows and asterisks next to the numbers denoted effects significantly deviated from zero with an alpha level of 0.05 (two-tail, Bonferroni-corrected), while the dashed arrows denoted those not. The number next to each arrow denoted the group average of that parameter. d. Exceedance Probability of each model in the extended model pool. Model 9 (the newly added model) is the winning model. e. Family exceedance probability of each family. The dorsal-to-ventral family became the winning family. f. Parameter estimations of the winning model, denoted with the same rules as Fig. 6c.

ducted a one-sample t -test on the individual parameter estimations of each of the two modulatory effects in the winning model to examine whether they consistently deviated from zero across participants (Fig. 6c). The results suggested that the modulatory effect of the familiar object pairs in the correct co-location condition significantly differed from zero ($t(29) = -3.42$, $p_{unc} = 0.002$, $dz = 0.62$, $MD = -0.46$) while that of the novel object pairs did not reach significance, $t(29) = -1.91$, $p_{unc} = 0.066$, $dz = 0.34$, $MD = -0.23$). Importantly, the modulatory effect of the action relations between the familiar objects was negative, i.e.

when the familiar object pairs were presented in the correct co-location, the connectivity between the ventral to the dorsal stream was weakened than when they were presented in the incorrect co-location condition.

Since the winning model emerged with the modulatory effects from the familiar-correct condition on this connectivity being negative, to further understand the dynamics predicted by the winning model, we conducted an unregistered exploratory analysis on the remaining parameters specified by this model i.e., the direct impact from the familiar-correct as well the novel-correct condition on both the ventral and the

dorsal ROI and from the novel-incorrect condition on the dorsal ROI, and the inherent connectivity from the ventral to the dorsal ROI. Consistent with the model specification, one-sample t -tests (two-tailed) revealed that the direct impact from the familiar-correct condition on both ROIs was significant and positive, suggesting an effect of action relations in the familiar object pairs on both ROIs (the red arrows in Fig. 6c); the direct impact from the novel-correct condition on the ventral ROI was significant and positive, suggesting an effect of action relations in the novel object pairs on ventral ROIs (the left yellow arrow in Fig. 6c). Further, though the direct impact from both the novel-correct and the novel-incorrect conditions on the dorsal ROI were significant and positive, paired sample t -test revealed that the direct impact from the novel-correct condition on the dorsal ROI was stronger than that from the novel-incorrect condition, suggesting that besides an effect on novelty (the middle and the right yellow arrows in Fig. 6c) an effect of action relations of the novel object pairs can be observed in the dorsal ROI ($t(29) = 3.11$, $p_{\text{unc}} = 0.003$, $d_z = 0.76$, $MD = 0.1$, the black horizontal line in Fig. 6c). Slightly surprisingly, one-sample t -test revealed that the inherent effective connectivity from the ventral to the dorsal ROI was not significant ($t(29) = -0.56$, $p_{\text{unc}} > 0.05$, the dashed gray arrow in Fig. 6c).

After noticing that the inherent effective connectivity was not significant in the winning model, and that the model with the second-highest protected model exceedance probability was a model specifying inherent effective connectivity of opposite direction (Model 5, see Fig. 6a), we considered the possibility that our data did not provide strong evidence of the direction of the inherent effective connectivity, and the winning model won because of its other structural features. The only difference other than the direction of inherent inter-ROI effective connectivity between Model 7 and 5 was the direct impact from the novel-incorrect condition to the dorsal ROI. Therefore, to reveal the specific feature that gives Model 7 superior fit to our data, we added a new model into the original model pool with a structure the same as that of Model 7 but specifying inherent effective connectivity of an opposite direction (Fig. 3), i.e., connectivity from the dorsal to the ventral ROI, to form an expanded model pool. The same DCM-based model comparison and parameter analysis was conducted with the expanded model pool. This time the newly-added model emerged as the winning model, with the model exceedance probability = 0.38 (Fig. 6d), the probability of equal model frequencies = 0.24, and the model family predicting effective connectivity from the dorsal to the ventral ROI emerged as the winning family (Fig. 6d). Parameter analysis revealed a dynamics in the new winning model very similar to that of the original winning model, with the modulatory effects of both the familiar object pairs in the correct co-location condition ($t(29) = -3.28$, $p_{\text{unc}} = 0.003$, $d_z = 0.60$, $MD = -0.43$) and the novel object pairs in the correct co-location condition ($t(29) = -2.85$, $p_{\text{unc}} = 0.008$, $d_z = 0.52$, $MD = -0.45$) being significantly negative. Also consistent with the original winning model, one-sample t -tests (two-tailed) revealed that the direct impact from the familiar-correct condition on both ROIs were significant and positive, suggesting the effect of action relations in the familiar object pairs on both ROIs (the red arrows in Fig. 6f), the direct impact from the novel-correct condition on the ventral ROI was significant and positive, suggesting the effect of action relations in the novel object pairs on ventral ROIs (the left yellow arrow in Fig. 6f), and that though both the direct impact from the novel-correct and the novel-incorrect conditions on the dorsal ROI were significant and positive, paired sample t -test revealed that again the direct impact from the novel-correct condition on the dorsal ROI was stronger than that from the novel-incorrect condition, suggesting an effect of action relations of the novel object pairs on the dorsal ROI ($t(29) = 2.64$, $p_{\text{unc}} = 0.010$, $d_z = 0.68$, $MD = 0.06$, the black horizontal line in Fig. 6f) in addition to the effect of novelty regardless action relation (the middle and the right yellow arrow in Fig. 6f). Also, the same as the original winning model, one-sample t -test revealed that the inherent effective connectivity between the ventral and the dorsal ROIs was not significant ($t(29) = 1.57$, $p_{\text{unc}} > 0.05$, the dashed gray arrow in Fig. 6f).

Besides ROI analysis, to further illustrate the scope of cortical regions responding to action relations, we conduct pre-registered exploratory second-level whole-brain voxel-wise analysis. It revealed that viewing familiar objects presented with apparent action relations led to increased activation in a set of occipitotemporal and parietal regions compared to when the action relation was not evident (familiar objects in correct co-location – familiar objects in incorrect co-location, $p = 0.001$ uncorrected, cluster-extent threshold of $p = 0.05$ corrected for family-wise error). These regions (Table 1) included bilateral inferior occipital gyrus and a dorsal cluster in the left superior parietal gyrus (Dice coefficient with corresponding AAL atlas = 0.11), extending towards the inferior parietal gyrus (Dice coefficient = 0.003). Viewing novel object pairs presented with visuo-spatially defined action relations, compared to when the action relation was not evident (novel objects in correct co-location – novel objects in incorrect co-location, $p = 0.001$ uncorrected, $FWE_c = 37$ voxels), led to increased activation in the bilateral inferior occipital gyrus, the left occipitotemporal cortex, the right middle occipital gyrus, the right superior parietal cortex (Dice coefficient with the AAL atlas of the right superior parietal gyrus = 0.16, and with the AAL atlas of the angular gyrus = 0.05) and the left superior (Dice coefficient = 0.12) and inferior parietal cortex (Dice coefficient = 0.07). Comparison between the thresholded activation maps (Fig. 7) revealed substantial overlap between the regions (Dice coefficient = 0.24), with four clusters responding to action relations in both the familiar and novel object pairs (Table 1). These clusters were observed in the bilateral occipital gyrus, the left occipitotemporal cortex and the left superior parietal gyrus (Dice coefficient with the AAL atlas of the left superior parietal gyrus = 0.02, and with the left inferior parietal gyrus = 0.003). The action relations in the novel object pairs activated larger regions in the left intraparietal sulcus than those activated by the familiar object pairs, and a cluster in the right intraparietal sulcus responded only to the action relations in the novel object pairs. A cluster in the left superior parietal gyrus, in contrast, responded only to the action relations in the familiar object pairs. The regions activated by action relations in the familiar object pairs, compared to those activated by action relations in the novel object pairs, were more dorsal in the left occipitotemporal regions, and more ventral in the bilateral inferior occipital cluster.

4. Discussion

With the sample size decided by a small pilot sample a priori, the present study provided direct fMRI evidence for the involvement of the dorsal visual stream in the automatic extraction of action relations and revealed that both the ventral and the dorsal visual streams respond to action relations in paired-object scenarios independent from object familiarity. Further, with DCM analysis, the present study suggests that action relations between objects in such scenarios reduce the effective connectivity between the two visual streams.

By demonstrating that both the ventral and the dorsal visual streams respond to action relations between objects, the present study extended previous studies on the ventral and the dorsal involvement in the perception of paired-object affordance in the context of object recognition (Roberts and Humphreys, 2010a; Roux-Sibilon et al., 2018). For the dorsal visual stream, such a result provided direct evidence of the dorsal visual stream's involvement in the automatic perception of action relations between objects, and is in line with existing understanding of the functional specialty of this visual stream (Goodale and Milner, 1992; Milner and Goodale, 2006, 2008; Yoon et al., 2002) and the results of a TMS study (Xu et al., 2017). Regarding the ventral visual stream, such involvement is in line with previous reports that the ventral visual stream also reflects information typically associated with the dorsal visual stream, such as actions towards objects, movement-related object properties (Almeida et al., 2013; Garcea et al., 2016; Kristensen et al., 2016; Mahon et al., 2013) and action relation between paired familiar objects (Bracci and Peelen, 2013; Buxbaum, 2017; Gallivan et al., 2014; Mahon et al., 2007; Roberts and Humphreys, 2010a; Roux-

Table 1

Clusters with increased activation when participants viewed familiar pairs with correct co-location compared to incorrect co-location ($p_{unc} < 0.001$, cluster-extent threshold of $p = 0.05$ corrected for family-wise error).

Familiarity	Region	MNI coordinates			z score	Cluster size
		x	y	z		
Familiar	Left inferior occipital gyrus	-18	-96	-15	5.87	92
	Left occipitotemporal cortex	-51	-66	3	5.41	118
	Right inferior occipital gyrus	30	-93	-12	4.97	52
	Left superior parietal gyrus	-18	-60	57	3.91	37
Novel	Left inferior occipital gyrus	-30	-93	-9	5.98	91
	Left occipitotemporal cortex	-48	-66	-9	5.13	59
	Right inferior occipital gyrus	30	-96	-9	4.99	45
	Left superior and inferior parietal gyri	-21	-57	45	4.23	66
	Right superior parietal gyrus	24	-63	54	3.95	81
	Right middle occipital gyrus	30	-84	30	3.76	37
Overlap	Left inferior occipital gyrus					29
	Right inferior occipital gyrus					17
	Left occipitotemporal cortex					27
	Left superior parietal gyrus					8

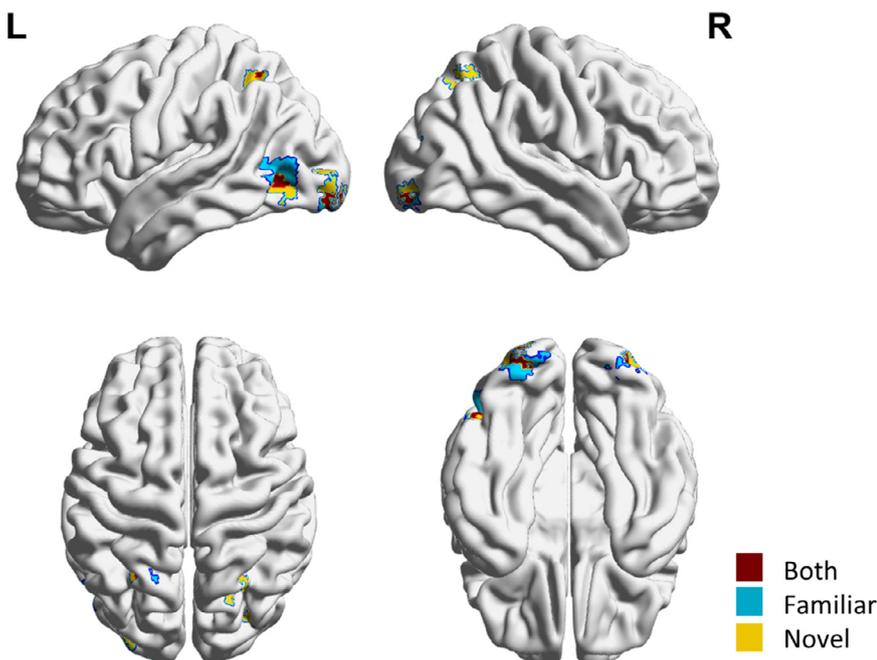


Fig. 7. The comparison between thresholded maps of regions activated by the action relation in the familiar (Blue), novel (Yellow) and both types (Red) of object pairs.

Sibilon et al., 2018). For instance, action relation between objects may co-varies with the presence of action-related structures, such as handles, which may further come from processing of surface and material properties of objects (Mahon & Almeida, under review) in the ventral stream. Such perception of graspable structures may be the source of the ventral responses to the relationship between the two objects in the present study, whether they are familiar or novel. The involvement of the ventral stream is particularly interesting in the light of our previous TMS study (Xu et al., 2017) which found that the ventral visual stream is not necessary for the processing of action relations, seemingly contradicting the results of the present study. It is unlikely that the activation change in the ventral stream observed in the present study was induced by the input from the dorsal stream, given the estimation of the dorsal-to-ventral inherent effective connectivity and the modulatory effect of action relations from our DCM analysis. A possibility is that some regions in the ventral visual stream do respond to the presence of action relations, probably by processing object properties that are important to define action relations, such as object co-location or other visual features co-varying with this manipulation, but such processing serves functions different from the dorsal response to the same manipulation. Unlike the

dorsal processing, these ventral stream areas do not directly affect immediate motor responses, i.e., would not be captured in the RTs of the TMS study. Such speculation is consistent with previous findings that the processing of action-related object properties in the ventral visual stream seems to contribute less to immediate manipulation of the objects than the dorsal visual stream (Cohen et al., 2009). Instead of supporting the motor-related or affordance-related functions as in the case of the dorsal visual stream, we speculate that the ventral-stream responses serve other functions, such as the formation of visual representation of objects or multiple-object scenes or the retrieval of semantic and functional knowledge of objects via object identification, which is consistent with the common understanding of the functionality of the ventral visual stream (e.g. Cohen et al., 2009; Goodale et al., 1994; Yoon et al., 2002).

An intriguing finding of the present study was that the ventral visual stream responds to visuo-spatially implied action relation between objects even when the active objects in the pair were not recognizable (the novel object condition). For these objects, the elevated activation in the ventral ROI cannot be attributed to the facilitated recognition at the object level, since in both correct- and incorrect- co-location condi-

tions the novel active objects remained unrecognizable by definition. A possibility is that the ventral visual stream responds to the more familiar layout of action-related structures in the correct co-location compared with the incorrect co-location condition. E.g., the handle of the novel active objects points towards the passive objects, while the incorrect co-location condition lacked such regularity. Such sensitivity of the ventral visual stream to the action-related structures has been reported in the case of elongation, a characteristic shape of manipulable tools (Chen et al., 2018). A further possibility is that the ventral visual stream responds to configural features of the object pairs indicated by the orientation of the action-related structures, with that of the active objects pointing the 'head' of the active objects towards the passive objects in the correct co-location conditions, while the incorrect co-location condition lacks such a clear configural organization. This speculation is consistent with previous reports of the involvement of the ventral visual stream in configural processing. For instance, it was found that the lateral and ventral occipitotemporal cortex not only represents the category of objects, but also their overall shapes (Bracci and Op de Beeck, 2016). Further, object pairs shown as interacting, compared with non-interacting depiction, elicit greater activity in the lateral occipital complex (Kim et al., 2011). In addition, it has been suggested that there is profuse inter-stream anatomical connectivity along the two visual streams, as well as rich within-stream connectivity between upper- and lower-stream regions in each visual stream. Therefore, it is still possible that the ventral ROI does receive input from the dorsal stream but not directly from the dorsal ROI we chose in the present study. The input might be relayed in one of the upper or lower-stream regions. Also, there might be feedback modulation from the frontal-parietal cortex to the lateral occipitotemporal cortex (Gallivan et al., 2013). For instance, the IPS has been found to modulate the low-level visual processing in the early visual areas (Liu et al., 2017) according to the action relations between objects, the effect of which may then be relayed to the ventral ROI.

Then, what is the functional relation between the ventral and the dorsal visual streams in processing the visuo-spatially defined action relations between objects according to our study? The data did not support a direct collaboration between the ventral and the dorsal visual streams in our task. Specifically, our DCM analysis suggested a negative modulation of action relationship on the (non-significant) inherent effective connectivity between visual streams. These results suggested that both the dorsal and the ventral visual streams might respond to visuo-spatially defined action relations, but subject this information to different computations, serving different functions. For instance, the ventral and the dorsal visual streams, due to their different functional specialty, work independently when the action relation between objects was not apparent, therefore we observe a non-significant inherent effect connectivity, but when an action relation between objects emerged as a result of our experimental manipulation, each visual stream responds to this manipulation and proceed to different computations to serve different functions (for instance, affordance extraction in the dorsal visual stream and representation formation/object recognition in the ventral visual stream), leading the originally independent neural activities in the two streams further deviate from each other, hence the negative modulation on their inherent effective connectivity. This speculation is similar to the proposal that the category-selective regions in the visual cortex are all integral parts of broad domain-specific networks (e.g., navigation, social categorization, etc.) and each contribute to the computations required in their corresponding networks (Mahon et al., 2007; Peelen and Downing, 2017). For instance, though both streams respond to the action-related experimental manipulation, this manipulation of a rather high-level feature might changes various sensory and perceptual features simultaneously, and the dorsal visual stream may extract stimuli change of its preferred kind to guide immediate object grasping and manipulation (Binkofski et al., 1998; Cohen et al., 2009; Culham et al., 2003; Frey et al., 2005; Rice et al., 2007; Tunik et al., 2005), whereas the ventral visual stream extracts its preferred kind but to gradually build visual representation of the objects and the scene of the objects for fu-

ture operation if a delay is introduced (Cohen et al., 2009; Goodale et al., 1994). Admittedly, this speculation is but one possible interpretation of our finding that the same manipulation may lead to dissociated neural activity among different brain regions, and future studies need to further differentiate parallel processing of the same stimuli from effective integration of information and collaboration between cortical regions.

Saying this, we would also like to note that the present study examined the perception of action relation of a very automatic and spontaneous kind. That is, the experimental task did not require any purposeful processing in terms of object recognition, action recognition or functional judgement, etc. in any of the experimental conditions. In contrast, the passive viewing task of the present study did not require inter-stream integration, therefore allows the two visual streams to independently respond to the visual stimuli and deviate from each other if their spontaneous responses to action relation between paired objects are indeed different. This might be a reason why the present study did not observe significant inherent connectivity between the two visual streams, nor positive modulation of the action relations on the inter-stream effective connectivity. We speculate that if the experimental task requires inter-stream integration (for instance, if the participants were explicitly required to make motor response based on both the co-location and the identity of the objects), information exchange would become necessary between the visual streams, and positive modulation of action-relation properties on inter-stream connectivity might become evident. Indeed, previous studies have suggested task dependence of the joint contribution of the ventral and the dorsal visual streams in processing paired-object affordance (Roux-Sibilon et al., 2018). Hence, it may be worth exploring how task settings modulate the relationship between the streams.

Taken together, our findings suggest that the functional relation between the dorsal and the ventral visual streams, though might be fueled by the same experimental manipulation, might dynamically change with task demands. Future study is needed to directly examine this possibility to further understand the functional relation between the two visual streams in processing the action-related object features and in various other cognitive tasks.

Data availability

Data supporting the reported analysis will be archived in the OpenNeuro project. This will include all raw and processed behavioral and fMRI data (anonymized) as well as analysis code, digital study materials, and laboratory log for all published results. The data will be archived according to the BIDS specifications. The approved Stage 1 protocol on the Open Science Framework (<https://osf.io/gty6q/>). The anonymized study data, digital materials/code and the laboratory log have been archived on OpenNeuro (dataset accession number: ds003696, version 1.0.0, <https://openneuro.org/datasets/ds003696/versions/1.0.0>).

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2021.118629](https://doi.org/10.1016/j.neuroimage.2021.118629).

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