scientific reports

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Visual perception of actions and objects has been shown to activate di erent cortical systems. Object recognition primarily relies on the ventral occipitotemporal cortex (VOTC)[1,2]; Action observation activates predominantly the occipitoparietal region, posterior dorsal temporal gyrus and the inferior frontal gyrus (IFG)[3,4]. VOTC has a well-established object "domain" organization, with di erent patches sensitive to several major, broad, evolutionarily-salient domains of objects (e.g., faces, animals, scenes and navigation-related large objects, small manipulable objects, with a broad animate/inanimate domain distinction)[5–7]. Although the interaction between the visual ventral and dorsal pathways (what vs. how/where)[8,9], which overlapped with part of the action perception network, has been well documented[10–18], the evidence about whether action perception and its communication with the ventral object regions is also guided by parallel processing-domain-structure (social purpose vs. object purpose) is less clear-cut.

Several lines of evidence have suggested a domain-related interaction pattern between object and action perception systems. Di erent domains of objects activate dorsal regions that are implicated in action perception: Manipulable objects activated the inferior parietal lobe (IPL)[19] supporting manipulation knowledge of tools and hand-object action perception[3,4,20–22]; faces and animals activated the posterior superior temporal sulcus (pSTS)[23] related to biological motion and social interaction perception[4,22,24,25]. e structural or resting-state functional brain connectivity of ventral-object and dorsal-action systems were also organized into a domain-like pattern:

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tool-preferring ventral areas were connected with the frontoparietal hand-arm/manipulation action processing regions[13,26–29], and face-preferring ventral areas with the pSTS social cognition region[30]. Functional connectivity (FC) between tool-preferring ventral and dorsal regions was enhanced during action-performing tasks[12,14]. Recent studies have further shown the causal in uence of the le inferior parietal areas on the ventral regions or object representations: lesions or stimulation to this region modulate the tool representations in the ventral-medial tool-preferring areas[31,32].

ese ndings are only indirect evidence for whether action perception system itself is organized by "domains" and how it communicates with the ventral object system dynamically. Given that the studies reviewed above tended to involve object stimuli (e.g., object names, movies of real multi-object contexts, but see Centelles et al.[24]), it is possible that these e ects were driven by object-domain properties (e.g., animate/biological vs. artifact object). Objects are recognized by the ventral visual system, which is organized by the salient object domains (i.e., animate/inanimate), and activate the typical action knowledge about that object stored in the dorsal system through brain connections, or activate the parietal regions directly through subcortical pathways[33,34]. It is thus not clear whether domains of actions are only organized along the animate/inanimate dimensions (a car moving vs. a person walking), or by domains that are beyond object properties, such as social-communicative-actions versus manipulation-actions[35]. For instance, pSTS has been robustly implicated in biological motion[36–39], but it is unknown whether this region has di erent degree of sensitivities to di erent kinds of biological motion (social- vs. manipulaiton-actions). Note that Centelles et al.[24] have tried to exclude the e ects of object properties and found stronger pSTS activations when participants watching two individuals interacting compared with two individuals acting independently using point-light stimuli. is comparison was between human-social-goal-directed versus non-goal-directed movements, whether pSTS di erentiate di erent goal-directed biological motions (human-directed social-communicative-actions vs. object-directed manipulation-actions) is unknown. Also unclear is whether action perception entails dynamic functional communications between the dorsal action perception network with the ventral object processing stream in a domain-speci c manner. Here, we test the hypothesis of a domain-organized action perception pathway using action stimuli excluding object domain differences, with an experiment designed to optimally evaluate both regional activities and task-based FC patterns. Participants watched videos of a human cartoon gure performing two types of actions (social-communicative-actions such as waving, manipulation-actions such as folding) to a same set of meaningless shapes during fMRI scanning. We examined whether the two action-perception conditions elicited di erent dorsal action perception system activations and whether such activations communicated with the ventral system di erently.

Results

Regional activities. Across all participants, both types of action perception conditions, compared to baseline, activated the bilateral IFG, superior parietal gyri, and posterior superior to inferior temporal gyri (voxel level $p < 0.0001$, cluster-extent FWE $p < 0.05$; Supplementary Fig. S1). We then carried out whole-brain univariate contrasts between conditions where participants watched videos of social-communicative-actions and manipulation-actions (voxel level $p < 0.0001$, cluster-extent FWE $p < 0.05$).

Social-communicative-actions video-watching. Social-communicative-actions, simulating human–human interaction such as waving, induced greater activation than manipulation-actions in the right precentral gyri (Prec), bilateral pSTS/posterior middle temporal gyrus (pMTG; Fig. 1a,c and Table 1).

Manipulation-actions video-watching. Manipulation-actions (e.g., folding an object) induced greater activation than social-communicative-actions in the bilateral supramarginal gyri (SMG), bilateral IPL, bilateral superior parietal lobe (SPL), bilateral postcentral gyri (Posc), bilateral Prec, right superior and inferior frontal gyri, and le insula (Fig. 1b,d and Table 1).

ese results indicate that social-communicative-actions and manipulation-actions, without object-domain information (same set of human cartoon gure and arbitrary meaningless shapes), elicited di erent distributed activations across frontal, parietal and dorsal temporal regions. Worth-noting is that both the social-communicative-actions and the manipulation-actions activated bilateral pSTS relative to baseline (Supplementary Fig. S1), in line with previous ndings that highlighted the role of pSTS in biological motions[36–39]. Importantly here, the pSTS showed stronger sensitivity to social-communicative-action perception, indicating e ects beyond biological motion per se. Also note that even though the cartoon gure and meaningless shapes may have some form changes during the actions (e.g., Fig. 2a, the form of the shape changes when the cartoon gure acts on it in the manipulation-action condition), these form changes do not correspond to the object domain di erences. ey did, however, result in more cumulative movement information in this condition than the social-communicative-actions (see "Experimental design" section). To examine if any results for the manipulation action were simply due to sensitivity to more visual changes (movements), we looked at the navigation condition that were not of interest in the current study, which had even higher cumulative movements than the manipulation-actions ($p = 1.185 \times 10^{-29}$). We compared the activation strengths in those manipulation speci c-activation regions between navigation condition and the manipulation-actions, with the rationale that if these regions simply responded to more actions, they should show higher responses to navigation than to manipulation actions. All but one of the manipulation speci c-activation clusters showed higher activations for the manipulation-actions or no di erences with the navigation, indicating that the manipulation-action-speci c e ects in these regions were not simply attributable to more movements in video stimuli (Supplementary Fig. S5a). e one exception located in the right IFG/Prec (MNI peak coordinates: 54, 9, 24), showing stronger activation in the navigation

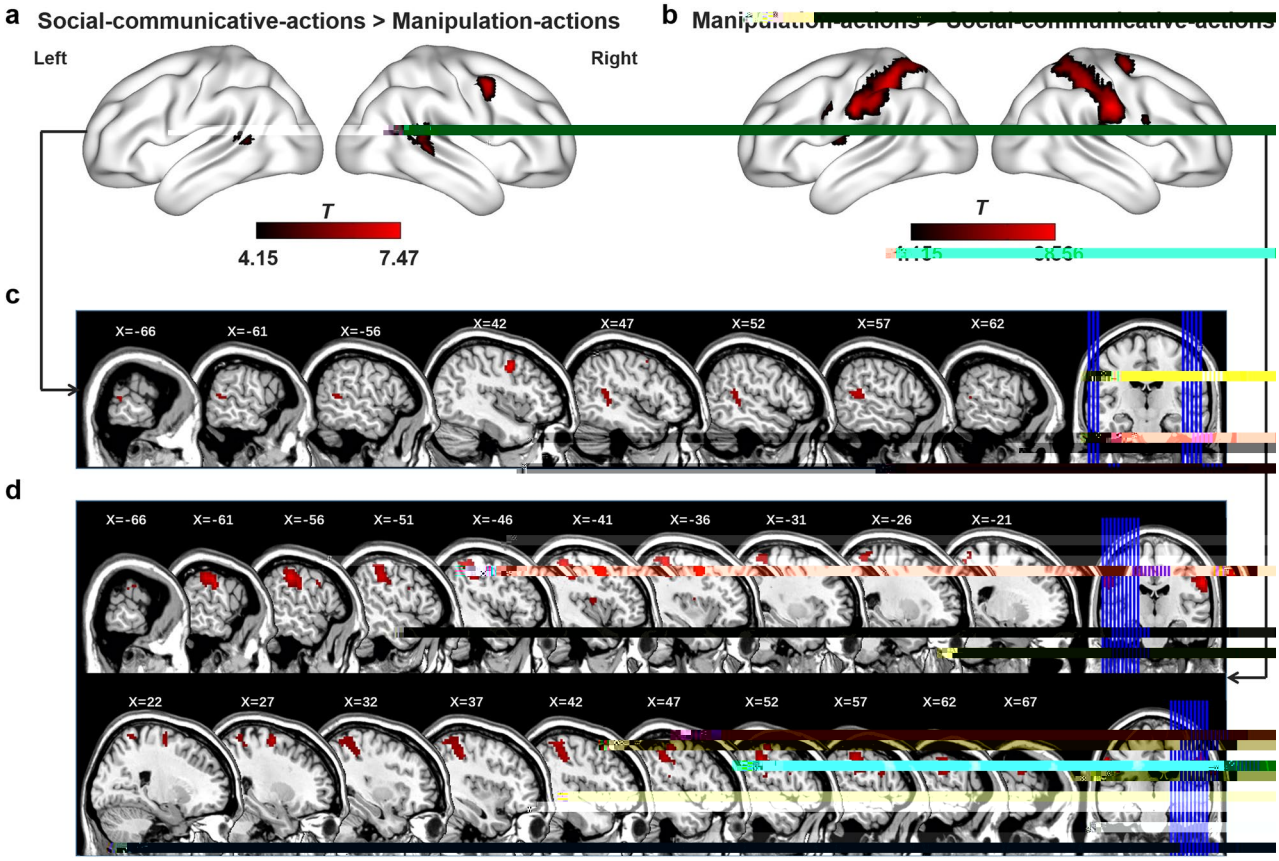


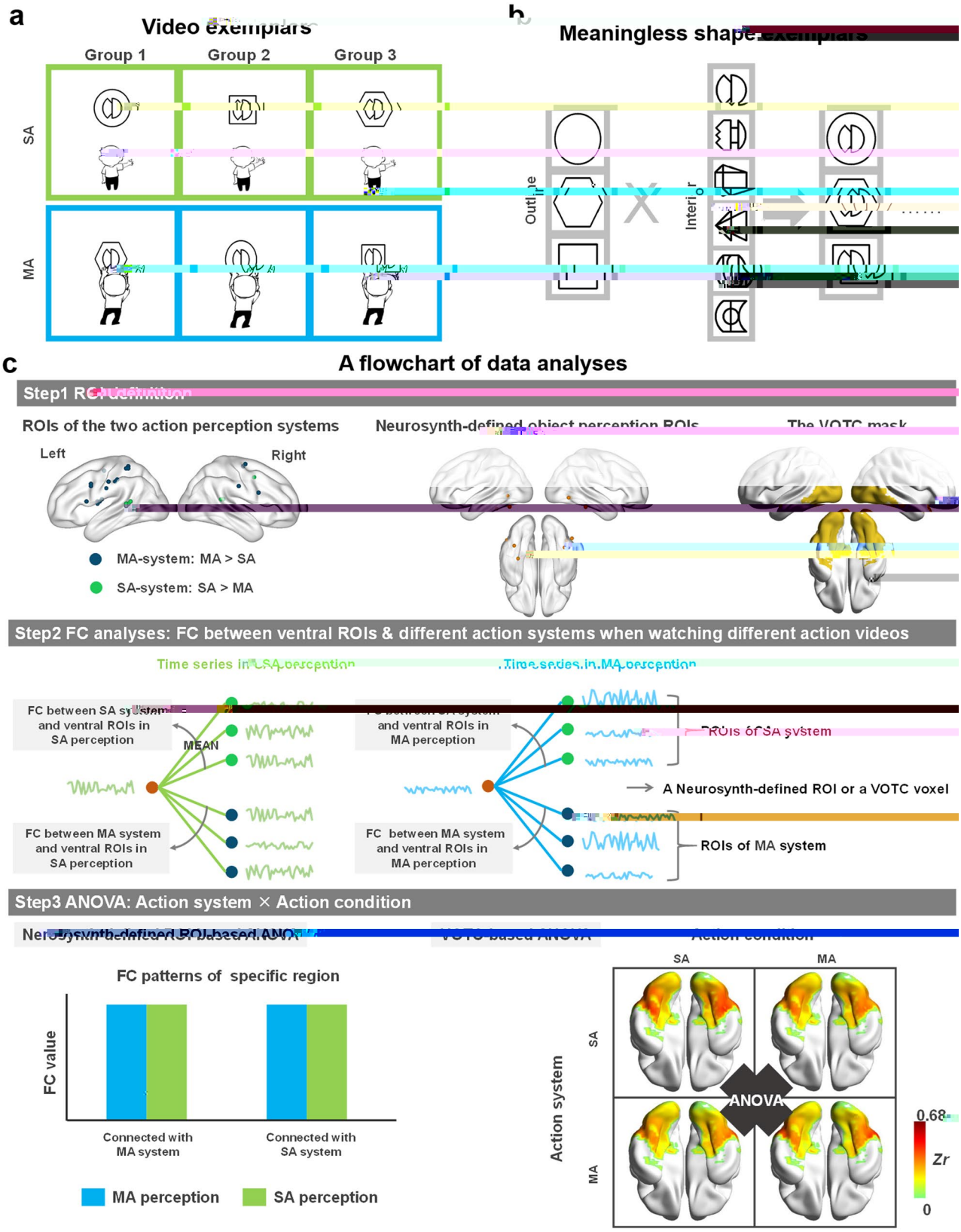
Figure 1. Whole brain univariate analysis results of social- and manipulation-action perception. **a**,**c** Cortical surface and multi-slice presentation of social-communicative-action speci c activation relative to the manipulation-action condition. **b**,**d** Cortical surface and multi-slice presentation manipulation-action speci c activation relative to the social-communicative-action condition. reshold: voxel level $p < 0.0001$, cluster-extent FWE corrected $p < 0.05$.

Contrast	Anatomical regions of the cluster's peak voxel (other including regions)	MNI coordinates of peak voxel (mm)			*t*	Cluster size
		x	y	z		
SA versus MA	Right Prec	42	3	45	7.47	43
	Right STG (MTG)	57	−42	15	5.73	71
	Le MTG	−66	−42	9	5.09	20
MA versus SA	Right Posc (IPL; SMG; SPL)	60	−18	33	8.56	459
	Le SPL (Posc; IPL, SMG)	−36	−45	60	8.17	462
	Right SFG (Prec)	27	−9	63	6.80	52
	Le Prec	−54	6	36	5.76	15
	Right IFoper (Prec)	54	9	24	5.46	21
	Le insular (rolandic oper)	−39	−6	12	5.10	16

Table 1. Whole-brain univariate analysis results of social- or manipulation-action-speci c activations. reshold: voxel level $p < 0.0001$, cluster-extent FWE corrected $p < 0.05$. *SA* social-communicative-actions, *MA* manipulation-actions, *Prec* precentral gyrus, *STG* superior temporal gyrus, *MTG* middle temporal gyrus, *Posc* postcentral gyrus, *IPL* inferior parietal lobe, *SMG* supramargical gyrus, *SPL* superior parietal lobe, *SFG* superior frontal gyrus, *IFoper* inferior frontal operculum.

than in the manipulation-actions. We thus performed additional validation analyses excluding this cluster in the FC analyses (ROI-based) below, and the results were fully replicated (Supplementary Fig. S5b–e).

[illegible] To explore whether and how the action perception system


a
Video exemplars
Group 1
Group 2
Group 3
SA
MA
b
Meaningless shape exemplars
Outline
Interior
c
A flowchart of data analyses
Step1 ROI definition
ROIs of the two action perception systems
Neurosynth-defined object perception ROIs
The VOTC mask
Left
Right
MA-system: MA > SA
SA-system: SA > MA
Step2 FC analyses: FC between ventral ROIs & different action systems when watching different action videos
Time series in SA perception
Time series in MA perception
FC between SA system and ventral ROIs in SA perception
MEAN
FC between MA system and ventral ROIs in SA perception
FC between MA system and ventral ROIs in MA perception
ROIs of SA system
A Neurosynth-defined ROI or a VOTC voxel
ROIs of MA system
Step3 ANOVA: Action system × Action condition
Neurosynth-defined ROI-based ANOVA
VOTC-based ANOVA
Action condition
FC patterns of specific region
FC value
Connected with MA system
Connected with SA system
MA perception
SA perception
SA
MA
Action system
ANOVA
0.68
Zr
0

communicates with the ventral object perception regions in a domain-speci c manner, we calculated the FC strength between the two action systems obtained for each participant (see "Methods" section) and VOTC in di erent task conditions. at is, for each Neurosynth-de ned object domain ROI (in the ROI analysis) or each VOTC voxel (in the whole VOTC mask analysis) we obtained four FC measures: FC strength with the two action systems (social-communicative-action and manipulation-action) in the two video conditions (social-communicative-action perception; manipulation-action perception) and applied a 2 × 2 repeated-measure ANOVA (Fig. 2c). Only those results showing statistical signi cance are reported below.

ROI analysis results. To examine whether action perception system connected with ventral object perception regions in a domain-speci c manner from a theory-driven perspective, analyses were carried out on VOTC ROIs showing face- or tool-preferring activations, de ned by Neurosynth meta-analyses (Fig. 3, Supplementary Table S4; see also Methods). Face preferring ROI (bilateral FFA) and tool preferring ROI (le LOTC) showed signi cant interaction e ects between action perception system and action viewing conditions (le FFA, $F(35) = 7.699$,

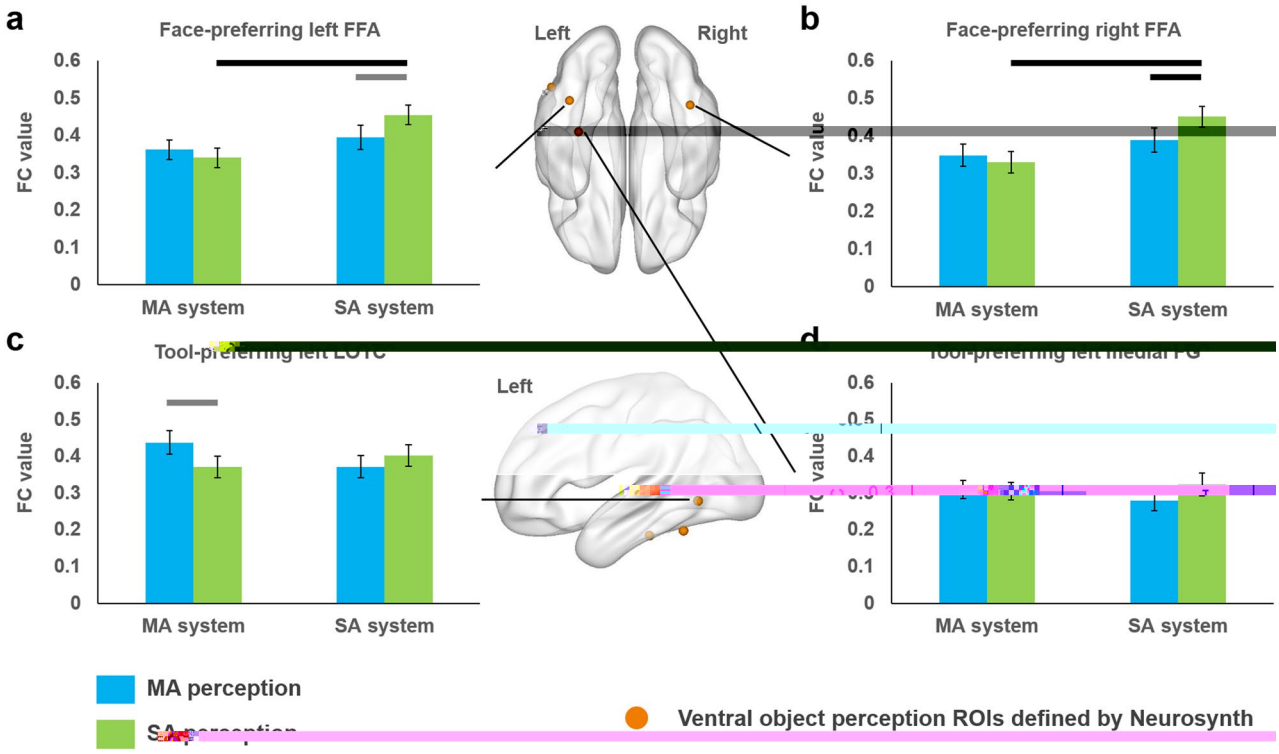


Figure 3. Results of Neurosynth-de ned ventral ROI-based ANOVA. **a**,**b** FC patterns of the face-preferring face fusiform area (FFA): Enhanced connection with the social-communicative-action system in social-communicative-action perception. **c** FC patterns of the tool-preferring le lateral occipitotemporal cortex (LOTC): Enhanced connection with the manipulation-action system in manipulation-action perception. **d** FC patterns of the tool-preferring le medial fusiform gyrus (medFG): no interaction e ects. We applied tests of simple e ects either within the same action system or within the same action condition for the Neurosynth-de ned ventral object perception ROIs showing signi cant interaction e ects; lines above bars indicate signi cant di erence between the two bars (black: adjusted $p < 0.05$; gray: uncorrected $p < 0.05$). *MA* manipulation-actions, *SA* social-communicative-actions.

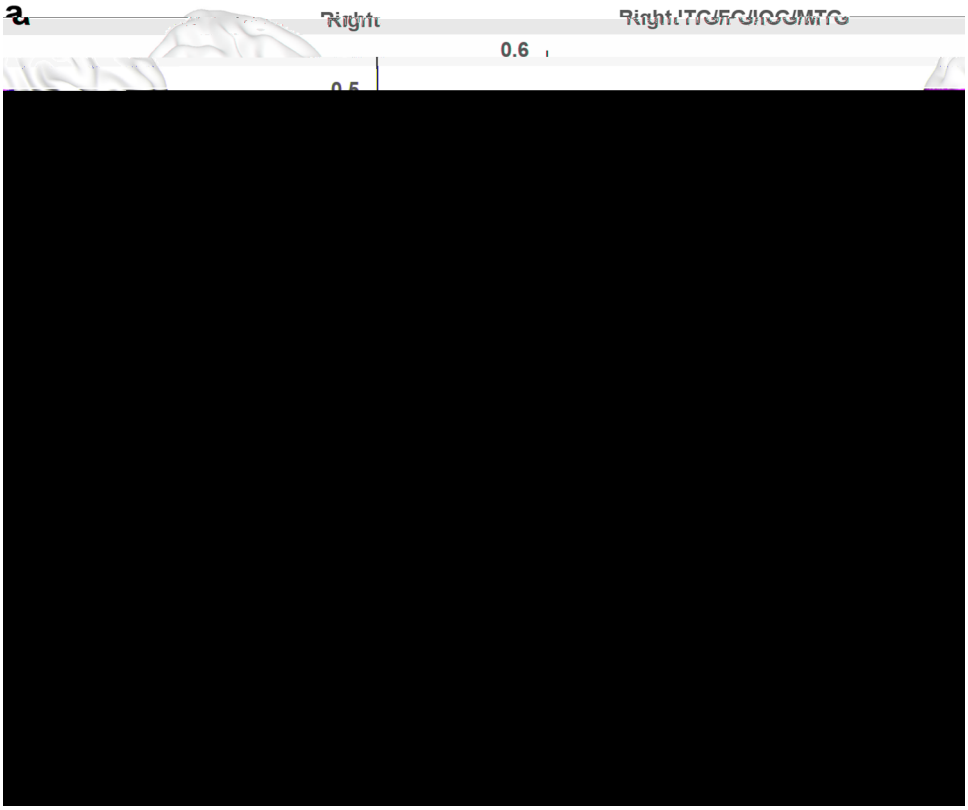
to manipulation-action system) during social-communicative-action perception and the relative activation strength (social-communicative-action perception minus manipulation-action perception) was highly signi - cant (Pearson R = 0.48, $p = 5.550 \times 10^{-225}$, Fig. 5a); Likewise, the correlation between the relative FC strength (to the manipulation-action system minus to the social-communicative-action system) during manipulation-action perception and the relative activation strength (manipulation-action perception minus social-communicative-action perception) was also signi cant (Pearson R = 0.486, $p = 3.934 \times 10^{-231}$, Fig. 5b).

c i i s ss o n

By excluding typical object-domain properties and manipulating human action contents, we tested whether action perception is processed by action domains of social- and manipulation-actions, and how action-perception regions communicate with the ventral visual pathway. ere were two main ndings. First, perception of social- and manipulation-actions elicits di erent activations in the parietal, frontal and superior temporal cortex, with social-communicative-actions such as waving activating the bilateral pSTS and right Prec, and manipulation-actions such as folding activating the bilateral SMG, IPL, SPL, Prec and Posc. Second, during action perception, these two systems communicate with the ventral system di erently (see summary in Fig. 6), with FC between the social-communicative-action system and the bilateral FFA enhanced during social-communicative-action perception, and FC between the manipulation-action system and le LOTC enhanced during manipulation-action perception. Whole VOTC analyses yielded cluster encompassing the right ITG and FG that showed a tendency to be modulated by both action conditions, with connection with one of the action systems stronger in the corresponding action condition than the other condition. Such action-domain-driven FC patterns converge with the object-domain distribution pattern in VOTC, with a signi cant correlation between the FC-with-action-system and local activity strength across VOTC voxels. Below we discuss these two ndings in turn.

c c m c i t i A a i e e i t a o n i d e n

Our s nding that social-communicative-action perception, relative to manipulation-action perception, elicits stronger activation in the bilateral pSTS, is consistent with previous studies of biological motion or communicative actions using real and point-light social-action videos[22,24,25,35,40,41]. e stronger right Prec region activation has been consistently observed in face-movement processing[4]. e e ects in this cluster might be because social-communicative-actions are o en accompanied



with face expressions (e.g., people o en smile when they wave to other people), this region might be activated by means of top down processing. For manipulation-action perception, the stronger activation in the SMG/IPL, SPL and Prec, is consistent with previous ndings when participants viewed transitive object-directed action videos[22] and human-object action perception[3,4] (meta-analyses). As reasoned in the Introduction, in these previous studies the actions were presented along with the entity properties. Our ndings, using the same set of human gures and meaningless shapes across social- and manipulation-action conditions, revealed that the sensitivity of these regions to social-communicative-action versus manipulation-action cannot be fully attrib-

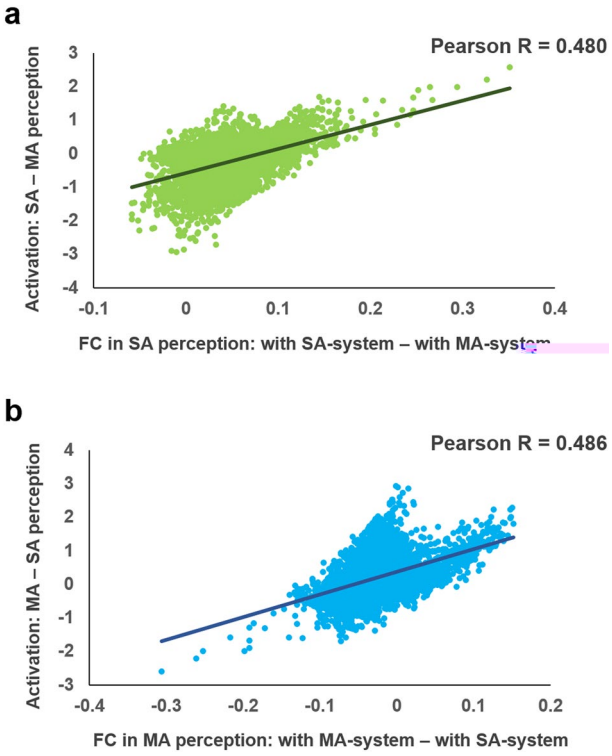


Figure 5. Correlation between the domain-speci c FC (connected with one of the action systems relative to the other one in the corresponding action perception condition) and domain-speci c local activation strength (in one action condition relative to the other) across VOTC voxels. Correlations for both domains (social vs. manipulation) were signi cant ($ps \leq 5.550 \times 10^{-225}$). Each dot represents a VOTC voxel ($N = 3915$), with green dots for the social-communicative-action domain and blue dots for the manipulation-action domain. *SA* social-communicative-action perception, *MA* manipulation-action perception.

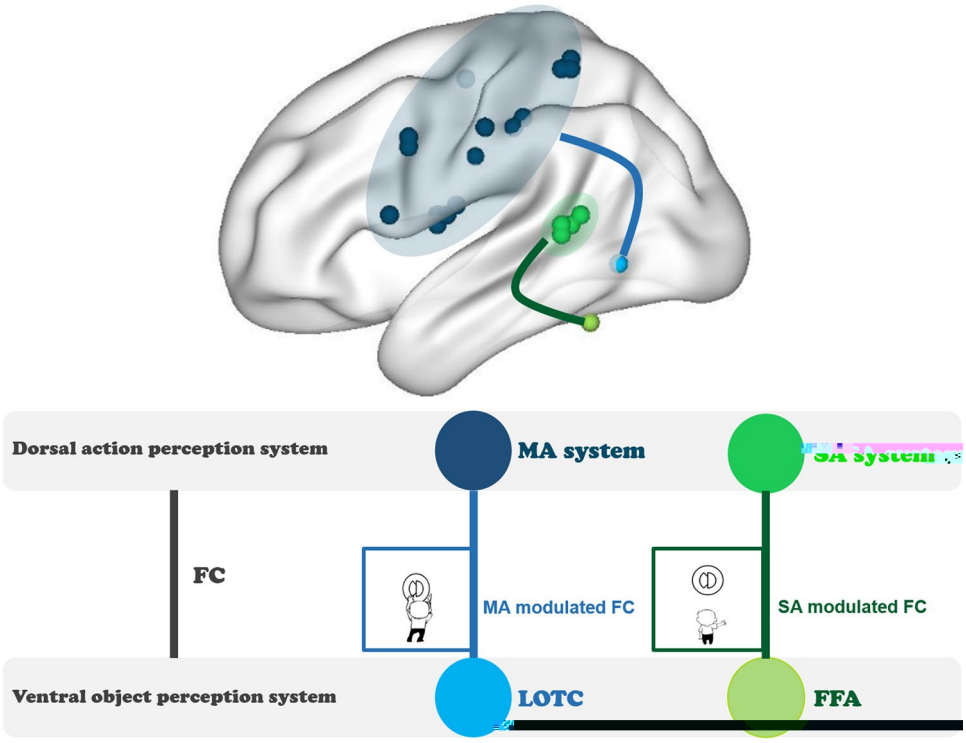


Figure 6. Summary of the FC patterns between the dorsal action perception system and the ventral object perception regions. *MA* manipulation-actions, *SA* social-communicative-actions.

uted to properties of the corresponding object domains (i.e., animate/biological vs. artifact shape properties), but related to the different types of action patterns or action consequences. Our manipulation-actions, in order to be natural, caused the target to go through a form change as a mechanical consequence of manipulation.

in the post-experimental survey of our study. Most of them named the meaningless shapes according to their shapes (e.g. diamond) and then establish relationship between the actions and shapes through rote learning.

Conclusion

The current results of social- versus manipulation-action domain organization in the action perceptual system (parietal, frontal, and dorsal temporal cortex), domain-specific functional-connection pattern with the ventral object pathway, together with the classical object domain-organization in the ventral visual pathway (faces in FFA vs. manipulable small objects in LOTC), reflect a unified principle in perception: social- versus manipulation- domains. This is in accord with the general notion of the connectivity-constrained domain representation hypothesis[47]. Previously, "domain" has been used usually in the context of object representation (conspecifics, tools, animals, etc.). Our findings highlight the significance of domains of human-interaction as an overarching principle: Object-manipulation and social-interaction for both ventral and dorsal visual perception system, and demonstrate domain-based dynamic functional communication across systems[48].

Materials and methods

Participants

Forty-four right-handed individuals (20 males; 22.4 ± 2.4 years old, range 18–28 years old) with normal or corrected-to-normal vision participated in this study. Thirty-six (15 males; 22.2 ± 2.4 years old, range 18–28 years old) of them were included in the following analyses. Eight participants were excluded for excessive head-motion and balance of the action-shape matching rules (see the following parts and Supplementary Table S1 for details). Results of using more liberal participant inclusion criteria using forty-two participants (i.e. excluding only the two participants with excessive head-motion) were largely similar (Supplementary Fig. S2). None reported psychiatric or neurological disorders. All participants gave written informed consent and were paid for their participation. The protocol was approved by the Institutional Review Board of the Beijing MRI Center for Brain Research. All methods were performed in accordance with relevant named guidelines and regulations.

Experimental stimuli

Participants viewed two kinds of action videos (social interaction and object-manipulation), with both the agent and object held constant (a human figure and an arbitrary meaningless shape). Videos were made by a professional animation company and included actions performed by the same cartoon figure towards the meaningless shapes (see Fig. 2a for screenshot; all video stimuli were shown in Supplementary Files). The actions correspond to two domains, with six actions in each type: social-communicative-actions (waving; saluting; bowing; kissing; clapping; greeting) and manipulation-actions (folding; tearing; overturning; rotating; pressing upper and lower; pressing left and right). The experiment also included a third navigation condition for other interests and were not considered for the main analyses. Each meaningless shape consisted of an outline and an interior shape (see exemplars in Fig. 2b). Six different interior meaningless shapes[49] were combined with three different outline shapes (hexagon, circle, and square) to form the meaningless shapes. To verify the sociality of the social-communicative-actions, we collected sociality ratings on a 7-point scale (how likely these actions are directed at people, 1 = never, 7 = always) in an independent group of participants ($N = 23$, 16 females, mean age = 22.9). The social-communicative-action condition was indeed rated to be significantly more person-directed than the manipulation-action condition [mean ratings 6.04 ± 0.65 vs. 3.02 ± 1.55; $t(22) = 9.104$, $p = 6.468 \times 10^{-9}$]. The participants were instructed to remember the correspondence between action and shape. They were asked to report the action name associated with the presented shape and simulate the action after scanning. The three types of meaningless shapes (outlines) were counterbalanced across action types in a between-participant fashion (Fig. 2a), such that meaningless shapes included in the different action types were fully matched at the group level. Equal number of participants in each action-shape matching group. It should be noted that in the manipulation-action condition, the action induced shape to change form, as an intrinsic consequence of manipulation. These visual shape changes made the cumulative movements significantly higher in the manipulation-action than the social-communicative-action condition (sum of the amount of changes of the whole stimuli for each frame relative to the previous one; absolute value of pixel changes: $p = 1.644 \times 10^{-7}$). While this difference (i.e., form changes of meaningless shape in the manipulation-actions but not in the social-communicative-actions) did not correspond to any known domain differences between inanimate and animate objects, we further considered the potential effects of this confounding variable (amount of visual changes) on action domain effects by looking at another condition of no-interest where the amount of visual changes were even greater than the manipulation action condition (see "Results" section).

A long-block experimental design was employed, with 36 time points for each block. This allowed enough number of time points to calculate time series correlation without needing to concatenate different blocks from the same condition. This design is optimal to evaluate both regional activities and task-based FC[50–52]. The video-watching task included 4 runs. Each run consisted of a 10 s fixation dot presented centrally, followed by 3 blocks from the different action conditions. Each block consisted of 24 trials from the same condition (i.e., each exemplar was repeated 4 times), followed by 10 s fixation. Each 3000-ms trial consisted of an action stimulus that lasted for 2000 ms, followed by 1000 ms of standing still (or running without turning in the navigation condition). The trial order was random and the block order was counterbalanced in a Latin square fashion across runs and participants. The experimental procedure was presented using Psychtoolbox (http://psychtoolbox.org/) implemented in MATLAB (https://www.mathworks.com/products/matlab.html).

Procedure and MRI data acquisition

The whole scanning session for each participant was about 95 min: (a) resting functional MRI scan; (b) meaningless shape viewing scan; (c) T1 functional scan; (d) video-watching scan (main experiment); (e) meaningless shape viewing scan; (f) diffusion tensor imaging. Data of procedure a, b, e, f were designed for another question and not analyzed herein. Whole scan data were acquired

using a Siemens Trio Tim 3-T scanner at the Beijing MRI Center for Brain Research. T1-weighted three-dimensional magnetization-prepared rapid gradient echo images were obtained in the sagittal plane (repetition time (TR) = 2530 ms, echo time (TE) = 3.39 ms, ip angle = 7°, slice thickness = 1.3 mm, slice gap = 0.65 mm, slice in-place resolution = 1.3 × 1.0 mm^2, eld of view (FOV) = 256 × 256 mm^2, slice number = 144). Functional images were acquired using an echo planar imaging sequence in the axial plane (TR = 2000 ms, TE = 30 ms, ip angle = 90°, slice thickness = 3.5 mm, slice gap = 0.7 mm, slice in-place resolution = 3.1 × 3.1 mm^2, FOV = 200 × 200 mm^2, slice number = 33). e scanner was upgraded during our experiment. All parameters remain the same except for the slice number (it was changed to 32 for technical reasons). We had decent number of participants before (N = 16) and a er (N = 20) the upgrade, and have looked at results separately, which had similar pattern to the combined (see Supplementary Fig. S3). We thus combined all participants as one group in the main analysis to improve power.

Functional images were preprocessed using Statistical Parametric Mapping (SPM12, http://www. l.ion.ucl.ac.uk/spm). e rst 5 volumes in each run were discarded. ree-dimensional head-motion correction was conducted with respect to the mean volume of each run. Two participants were excluded for excessive head motion (above 2 mm or 2°). No other participants exhibited excessive head motion (< 1.47 mm or 1.11°). For each participant, T1 images were co-registered to their mean functional images and were subsequently segmented. Functional images were normalized to the Montreal Neurological Institute (MNI) space using T1 image uni ed segmentation. A er normalization, functional images were resampled to 3 × 3 × 3 mm^3 and spatially smoothed with a 6 mm Full Width Half Maximum Gaussian lter. For FC analyses, the following preprocessing steps were additionally performed: linear trend removal, band-pass ltering (0.01–0.1 Hz), and regression of eight nuisance covariates (six rigid-body head-motion parameters, white matter signal, and cerebrospinal uid signal). Global signal regression is controversial[53,54] and o en causes 'negative' correlations among brain regions. erefore, we did connectivity analyses using data without global signal removal and repeated the analyses with global signal regression as validation analyses (see validation results in Supplementary Figs. S6 and S7; Supplementary Table S2). e residual time series with these nuisance covariates regression were used to do FC analyses.

[illegible] First, we carried out whole-brain univariate analysis for the video-watching task to test whether social-communicative-actions and manipulation-actions would lead to di erential brain activity. e whole-brain analyses were conducted using SPM12. In the rst-level analysis, all preprocessed functional data were analyzed using a general linear model (GLM). We included nine predictors: the three video-watching experimental conditions and six motion parameters. e default value of the high-pass lter (128 s) was used to remove confounding in uences on the BOLD signal, such as physiological noise from cardiac and respiratory cycles. Contrasts between social-communicative-actions and manipulation-actions, and between social- or manipulation-actions relative to baselines were built and computed for each participant. en, in the second-level analysis, one-sample t-test analyses were applied to compare the mean activation across participants with zero (threshold set as voxel level $p < 0.0001$, cluster-extent FWE corrected $p < 0.05$). In this step, we used a gray matter mask that included voxels with a probability higher than 0.4 in the SPM5 gray matter template. All of the surface brain maps in the present study were visualized with the BrainNet Viewer[55] (http://www.nitrc.org/projects/bnv/).

[illegible] To explore how the dorsal-stream action perception systems communicate with the ventral object perception regions during action perception, we carried out task-state FC analyses. Speci cally, we calculated the FC, seeding from the social- or manipulation-action perception systems, with ventral object perception regions during the two video conditions. We then applied repeated-measure ANOVAs to these FC measures. Figure 2c shows a owchart of these analyses.

Region of interest (ROI) de nition. Given that we did not have an independent localizer scan, we de ned the social- and manipulation-action ROIs using a leave-one-participant out approach, so that the action perception systems de nition data was independent from the FC analyses. We used N-1 participants to run the whole brain univariate contrast analyses (social-communicative-action perception vs. manipulation-action perception) and used the peak voxels to de ne action system ROIs for that remaining participant. Iterating this procedure 36 times de ned the two sets of action system ROIs for each participant. We then used those peaks to form 3 mm radius sphere action perception ROIs (Fig. 2c; All peak coordinates presented in Supplementary Table S4). ree out of the 31 ROIs across all iterations were within VOTC and were excluded.

We considered ventral object perception regions in two ways: (1) In a ROI approach, we de ned classical regions showing preference for social entities and manipulable objects/tools using the Neurosynth meta-analyses platform (https://neurosynth.org). Speci cally, we searched for the terms "face" and "tool" separately in Neurosynth and retrieved the association threshold maps (896 studies including the word "face" and "115" studied including the word "tools"; default threshold at FDR corrected, $p < 0.01$). It should be noted that we also used "artifacts" or "manipulable objects" to search, but no results were found. We used "tools" rather than "objects" because the former is more speci c to manipulation actions. ese maps were resliced into the same voxel size with the functional images, i.e., 3 × 3 × 3 mm^3. e strongest peaks within VOTC for "face" were in the bilateral lateral fusiform gyrus (i.e., fusiform face area, FFA), and for "tools" in the le lateral occipitotemporal cortex (LOTC; Supplementary Fig. S4; Table S4). ese peaks were extracted and used to form sphere ROIs of 3 mm radius. A small signi cant cluster for tool in the medial fusiform gyrus (medFG) was further included given its relevance highlighted in previous literature[12,29,56]; (2) in a data-driven approach, we used a whole VOTC mask,

obtained using previous dataset in our lab, to test the dynamic FC patterns of dorsal action perception system and ventral object perception system. It was de ned by combining functional and anatomical localization, including regions that were activated during an object picture perception task within the occipitotemporal cortex (z coordinate below 10; see Wang et al.[57], procedure following Kriegeskorte et al.[58]).

FC computation. e following steps were carried out in each participant separately. First, the task-state residual time series of each run was segmented into separate conditions as follows: for each block in each run, the rst 4 volumes (8 s) were discarded, and 2 volumes (4 s) of the 10 s xation were included to account for the hemodynamic delay. Within each ROI sphere of the action systems, the residual time series of all voxels were averaged. en, we computed the FCs seeding from each social- or manipulation-action perception ROI sphere with each Neurosynth-de ned ventral object domain ROI (in the ROI analysis), or each voxel in the VOTC mask (in the Whole VOTC mask analysis), under the two action perception conditions separately. e correlation coe cients were then Fisher-z transformed and averaged across all ROIs within an action system, across all runs within an experiment condition, to yield four measures for each ventral ROI or voxel (Fig. 2c): FC with the social-communicative-action system in the social-communicative-action condition, FC with the social-communicative-action system in the manipulation action condition, FC with the manipulation-action system in the social-communicative-action condition, FC with the manipulation-action system in the manipulation-action condition. Note that in the main analysis, multiple ROIs in the same action systems were averaged together for the ANOVA analysis. We also report the FC results between each separate action perception ROI sphere and each Neurosynth-de ned object perception ROI (Supplementary Fig. S9).

ANOVA. For Neurosynth-de ned ventral classical object perception ROIs, we applied repeated-measure ANOVAs using SPSS Statistics 20 (https://www.ibm.com/cn-zh/analytics/spss-statistics-so ware) to test whether social- and manipulation-action perception systems interact with face and tool perception regions in a domain-speci c way. We then applied repeated-measure ANOVAs using SPM12 to identify brain regions showing signi cant main e ects of action brain system/action perception condition or interaction e ects between the action brain system and action perception condition within whole VOTC mask (threshold set as voxel level $p < 0.001$, cluster-extent FWE corrected $p < 0.05$). For regions showing signi cant interaction e ects, subsequent comparisons were performed (two-tailed paired-sample t-tests) to test the speci c connection patterns among the four FC conditions (all Bonferroni-corrected based on four comparisons of simple e ects).

T RCli Ceica Owtc e ree V wi strnpF hTb tca acCsi et e Ct sdy e apnVl p lietsa as rv i t at te To examine whether dorsal action systems could a ect the VOTC activation through functional coupling when object-domain information had been well-controlled, we calculated the correlation between FC strength with a speci c action system and activation strength in each action perception conditions across VOTC voxels. First, for each VOTC voxel we calculated its average FC strength across all participants for each of the four measures (with two action systems in two conditions). en, for each VOTC voxel we calculated the average activation strength across participants for social-communicative-action and manipulation-action perception conditions separately. en we computed the Pearson correlation coe cient between the domain-speci c FC strength (i.e., connected with one of the action systems relative to the other one in the same action perception condition) and the domain-speci c activation strength (i.e., in one action condition relative to the other) across all of the VOTC voxels.

v t i aiaad ata y b

e data that support the results of the present study are available from the corresponding author upon reasonable request.

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Y.B. and Z.H. designed the experiment. H.Y. and C.H. did data acquisition and analysis. Y.B. and H.Y. dra ed the paper and substantively revised it.

C m r i ti e t te e op gn n s s

e authors declare no competing interests.

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