

A common and specialized neural code for social attention triggered by eye gaze and biological motion

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ABSTRACT

Humans appear to be endowed with the ability to readily share attention with interactive partners through the utilization of social direction cues, such as eye gaze and biological motion (BM). Here, we investigated the specialized brain mechanism underlying this fundamental social attention ability by incorporating different types of social (i.e., BM, gaze) and non-social (arrow) cues and combining functional magnetic resonance imaging (fMRI) with a modified central cueing paradigm. Using multi-voxel pattern analysis (MVPA), we found that although gaze- and BM-mediated attentional orienting could be decoded from neural activity in a wide range of brain areas, only the right anterior and posterior superior temporal sulcus (aSTS and pSTS) could specifically decode attentional orienting triggered by social but not non-social cues. Critically, cross-category MVPA further revealed that social attention could be decoded across BM and gaze cues in the right STS and the right superior temporal gyrus (STG). However, these regions could not decode attentional orienting across social and non-social cues. These findings together provide evidence for the existence of a specialized social attention module in the human brain, with the right STS/STG being the critical neural site dedicated to social attention.

1. Introduction

Sharing attention with interactive social partners, referred to as social attention, plays an important role in human adaptive functioning and interpersonal communication (Birmingham and Kingstone, 2009; Frischi et al., 2007; Klein et al., 2009). This indispensable capability enables people to accurately detect in a timely manner what others are focusing on and to further infer their inner states and predict future behaviors (Klein et al., 2009; Nummenmaa and Calder, 2009). Such ability develops in early life (Farroni et al., 2004; Hood et al., 1998) and promotes the development of socio-cognitive skills (e.g., theory-of-mind, Brooks and Meltzoff, 2005; Shepherd, 2010). However, this social attention ability is impaired in individuals with autism spectrum disorder marked by striking social deficits (Dawson et al., 2012; Goldberg et al., 2008; Ristic et al., 2005). A modified central cueing task has been widely used to explore the characteristics and mechanisms of social attention (Friesen and Kingstone, 1998). In this task, a nonpredictive social cue (e.g., gaze) is presented at the center of the screen. This social cue induces a reflexive attentional orienting effect, as evidenced by facilitated responses to peripheral targets presented on the same side indicated by the social cue than those presented

on the opposite side. This effect occurs at an early stage (as early as 100 ms after cue onset) and even if the cue is counter-predictive of the target location, thus revealing its reflexive nature (Driver et al., 1999; Friesen et al., 2004; Friesen and Kingstone, 1998; Frischi et al., 2007; Langton and Bruce, 1999). Although the social cues are presented centrally like the conventional endogenous cues, the direction of these cues are not predictive or even counter-predictive of the target position (Driver et al., 1999; Friesen et al., 2004). On the other hand, social attention is likewise distinct from exogenous attention, as it is not triggered by cues in the periphery and exhibits a significantly delayed inhibition of return (Frischi et al., 2007). Therefore, we can speculate that such reflexive social attention represents a special form of spatial attention that is different from traditionally identified types of covert attention (i.e., exogenous and endogenous). While a clear double dissociation would be necessary to corroborate this claim beyond speculation, this perspective offers an opportunity to probe human visual attention from a new viewpoint (Friesen and Kingstone, 2003; Kingstone et al., 2000).

Eye gaze, as the 'window to the mind', delivers other people's internal state and serves as a salient social attention cue (Tier and Batty, 2009; Langton et al., 2000). There is plenty of research showing that eye gaze can automatically direct our focus of attention (Friesen and

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Kingstone, 2003, 1998; Ji et al., 2020; Wang et al., 2020; Yang et al., 2024; Zhang et al., 2025). Interestingly, this gaze-triggered reflexive attentional effect is also presented in nonhuman primates, implying that an evolutionary basis might exist for the mechanism of social attention effect (Deaner and Platt, 2003). The preservation of this ability across species increases the likelihood that gaze-triggered attentional orienting might conceivably involve some specialized mechanisms dedicated to identify where gaze is directed in the environment (eye-direction detector), as implied by Baron-Cohen (1996). Further research into the brain mechanisms of the gaze-triggered attentional effect has revealed the involvement of distributed brain regions. Some studies have suggested the engagement of the ventral attention network (e.g., inferior parietal lobe (IPL), and inferior frontal gyrus (IFG) in gaze cueing effect (Sato et al., 2016). However, other studies have reported the involvement of the dorsal attention network (e.g., superior frontal gyrus (SFG), and precentral) in modulating the attentional effect induced by gaze (Greene et al., 2011; Joseph et al., 2015). Furthermore, these previous studies also yield inconsistent conclusions as to whether the STS/STG, which has been assigned functions in mental state and social cognition (Carlin et al., 2012; Zelinková et al., 2013), was involved in gaze-mediated attentional effect (Engell et al., 2010; Hietanen et al., 2006; Nummenmaa and Calder, 2009; Sato et al., 2009; Vaidya et al., 2011). Therefore, the exact brain mechanisms underlying the gaze-triggered attentional effect remains equivocal.

As another type of social cue, walking direction of point-light biological motion (BM) varied significantly in physical features from eye gaze: it is portrayed by only a handful of point-light dots attached to the main joints of a person (Grossman et al., 2000; Johansson, 1973; Troje, 2002). Similarly, BM cues can induce a reflexive attention orienting effect (Shi et al., 2010). This effect also emerges early in development, and even occurs with only the feet motion cues and independent of

observers' subjective awareness of the biological nature (Wang et al., 2014). It has hence been suggested that there may exist a specialized brain mechanism sensitive to the direction of BM (i.e. 'life motion detector'), which is analogous to the eye-direction detector (Johnson, 2006; Troje and Westhoff, 2006; Wang et al., 2014). While the neural mechanism of gaze-mediated attentional orienting has already been investigated by several neuroimaging studies (Engell et al., 2010; Hietanen et al., 2006; Sato et al., 2016, 2009), it remains largely unknown concerning the exact neural basis subserving BM-mediated attentional orienting. Further, a more intriguing question is whether the BM- and gaze-mediated attention effects share common underlying neural mechanisms. Notably, our latest behavioral study has revealed that the emotional information modulated the gaze- and BM-mediated attentional orienting effect in a similar manner (Yuan et al., 2023). In addition, our recent behavioral genetic study has demonstrated that these two types of social attention effects have shared genetic bases (Wang et al., 2020). Furthermore, we found a robust cross-category adaptation effect between gaze- and BM-mediated orienting, indicating that common neural substrates might be involved in triggering these two different types of social attention behavior (Ji et al., 2020). In light of all the aforementioned evidence, we proposed the existence of a general and shared 'social attention detector' in the human brain, combining information regarding others' focus of attention from various social signals. However, where such detector is located in the brain has not yet been explored.

To directly address these issues, the present study investigated the common and unique neural basis underlying social attention by adopting the functional magnetic resonance imaging (fMRI) technique in conjunction with the modified central cueing task. By introducing the two different types of social cues (i.e., BM and gaze) to the modified central cueing task (Fig. 1), we examined the common neural

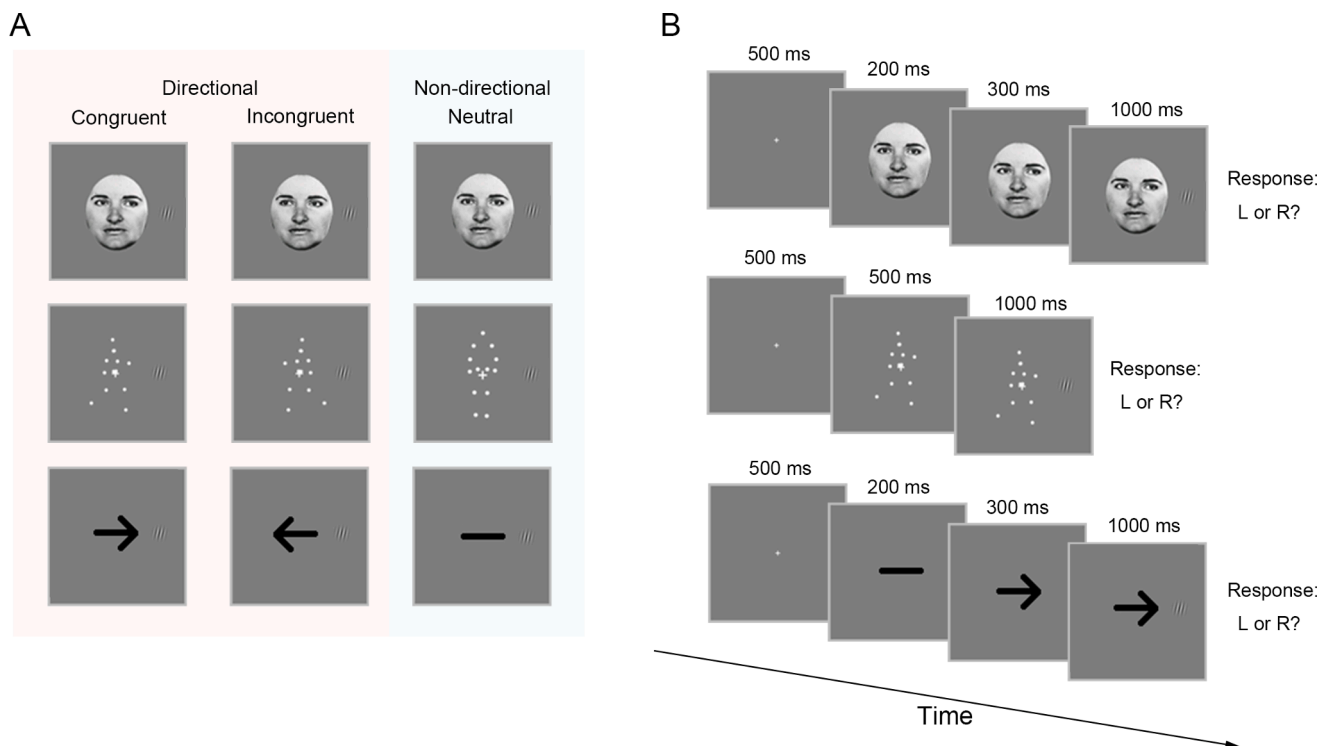


Fig. 1. Experimental flow. (A) Sample of directional (i.e., congruent and incongruent) and non-directional cues for the gaze cueing, BM cueing, and arrow cueing tasks. (B) Illustrations of trial sequences in the gaze cueing, BM cueing, and arrow cueing tasks. In the gaze cueing task, after 500 ms, a face with straight (non-directional) gaze was presented for 200 ms. Then an averted (directional) face was displayed for 300 ms. After that, a small Gabor patch appeared as a probe on the left or right side of the fixation. Observers were required to indicate the location of the probe by pressing one of two buttons as quickly as possible while ensuring accuracy. The procedure of the BM cueing task was similar to that of the gaze cueing task with the variation being that a point-light walker (directional or non-directional) was presented for 500 ms. The arrow cueing task was identical to the gaze cueing task except that arrows (directional) or straight lines (non-directional) were used as central cues.

mechanisms underlying different types of social attention behavior. In addition to the social cues, a non-social stimulus (i.e., arrow), which can also trigger attentional orienting effects (Hietanen et al., 2006; Joseph et al., 2015), was included as a comparative cue. The comparison of brain representations for social and non-social attention would provide a unique opportunity to probe the specialized neural mechanisms tuned to social attention. Notably, we used a multivariate decoding approach (multi-voxel pattern analysis, MVPA) to identify the neural organization of the attention effects triggered by BM, gaze, and arrow cues. The MVPA method, extracting information from patterns of activation across a set of voxels, has been proven as a more sensitive and quantitative tool for characterizing the neural representation of a specific cognitive process (Norman et al., 2006; Peelen and Downing, 2007). In addition to within-category MVPA, we also performed cross-category MVPA to explore the dedicated and common neural mechanisms that can be shared across different social (BM and gaze) but not non-social (arrow) cues.

2. Materials and methods

2.1. Participants

Twenty-three volunteers (14 females) aged between 18 and 27 years (mean age = 24.04, SD = 2.21) participated in this study. Two participants were excluded due to excessive head motion (>2 mm of maximal translation in any direction of x, y, or z or 2° of any angular motion throughout the scan). All of them had normal or corrected-to-normal vision with no history of neurological or psychiatric disorders. They have given written informed consent in accordance with the procedure and protocols approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences. All participants were naïve to the purpose of the experiments and received financial rewards after the experiment.

2.2. Materials and procedures

Stimuli were generated and displayed on a gray background using MATLAB together with the Psychophysics Toolbox (Brainard, 1997). For the gaze cueing task, neutral faces with averted (directional) or straight (non-directional) gaze were used. Specifically, a female face image was taken from Ekman and Friesen's Pictures of Facial Affect (Ekman and Friesen, 1976), and it was cropped to remove features outside of the face (e.g., hair and ears). The gaze direction was manipulated by using the Photoshop software. For the BM cueing task, the point-light BM sequence comprised 13 dots depicting the motions of markers attached to the head and the major joints were adopted from a previous study and created by capturing the motion of a walking actor (Vanrie and Verfaillie, 2004). Each gait cycle of the BM stimulus was 1 s and contained 30 frames, which displayed stationary walking and did not contain any overall translational motion. The BM stimuli facing leftwards or rightwards were adopted as the directional cues, and the BM stimulus presented in frontal view was employed as the non-directional cue. The initial frame of the point-light display was randomized for each trial to avoid observer's anticipation. For the arrow cueing task, arrows were created by combining a straight line and an arrowhead attached to the leading end of the line. A straight line without arrowheads was utilized as the non-directional cue (Fig. 1A).

In the scanner, participants completed the gaze cueing, BM cueing, and arrow cueing tasks, and the experimental conditions was counter-balanced across participants. Stimuli were projected on a 27-inch screen outside the MRI scanner. Participants viewed them through a tilted mirror mounted on the head coil. The viewing distance was about 75 cm. We used an event-related design with a total run duration of 306 s.

Each participant performed 9 runs, consisting of 3 gaze cueing task runs, 3 BM cueing task runs, and 3 arrow cueing task runs. There were 60 trials in each run, including 18 congruent trials (the target location

and the cue direction were the same), 18 incongruent trials (the target location and the cue direction were opposite to each other), 18 neutral trials (non-directional), and 6 catch trials. Each trial lasted for 2 s, and the inter-trial interval was jittered between 2 s and 6 s. The presentation sequence was generated by Optseq2 (Dale, 1999).

Specifically, in the gaze cueing task, each trial began with fixation on a central cross ($0.6^\circ \times 0.6^\circ$) within a frame ($15.1^\circ \times 15.1^\circ$) that extended beyond the outer border of the stimuli. After 500 ms, a face with straight gaze (subtended $3.7^\circ \times 4.8^\circ$ in visual angle) was presented for 200 ms. Then, the face stayed unchanged (non-directional) or shifted its gaze leftwards or rightwards (directional) for 300ms. After the cue presentation, a target (i.e., Gabor patch) appeared on the left or right side of the screen at a distance of 3.8° from the fixation. Both the cue and the target remained on the screen for 1000 ms, during which participants were required to indicate the location of the target by pressing one of the two keys on a keyboard as quickly and accurately as possible. Throughout the task, a central cross was always displayed at the center of the screen, and participants were asked to fixate on the central cross from the beginning of each trial. Participants were explicitly told before the experiment that the cue direction was not predictive of the target location.

In accordance with previous studies (Ji et al., 2020; Liu et al., 2021; Shi et al., 2010; Wang et al., 2020, 2014; Zhao et al., 2014), the BM cueing task was similar to that of the gaze cueing task with the variation being that a point-light BM stimulus with averted (directional) or straight (non-directional) walking direction ($2.4^\circ \times 5.2^\circ$) was employed as central cue and presented for 500 ms. The procedure of the arrow cueing task was identical to that of the gaze cueing task except that gaze cues were replaced by arrow cues. That is, a straight line was displayed for 200 ms, followed by a directional (left or right arrow, $1.2^\circ \times 1^\circ$) or non-directional (a straight line) cue that was shown for 300 ms (Fig. 1B). It should be noted that the procedures for gaze and arrow cues were established based on the consideration that the BM stimulus is dynamic, whereas the gaze and arrow stimuli are static. In order to make these three types of cues more comparable in terms of dynamics, researchers often add a non-directional stimulus to simulate the perception of motion involving eye gaze and arrow cues (Lachat et al., 2012; Ulloa et al., 2018).

2.3. Imaging acquisition

Functional and anatomical data were collected using a 3-Tesla Siemens Prisma scanner with 64-channel head coil at the Beijing Magnetic Resonance Imaging Center for Brain Research. Functional data were collected using a T2*-weighted echo planar imaging (EPI) sequence with the following parameters: 78 axial slices (with multi-band), TR = 2000 ms, TE = 30 ms, flip angle = 70° , FOV = 192×192 mm², matrix size = 96×96 , thickness/gap = 2/0 mm. A fMRI run in each task consists of 150 functional volumes. A 3D T1-weighted magnetization-prepared rapid gradient echo (MP-RAGE) image was acquired with the following parameters: 128 sagittal slices, TR = 2600 ms, TE = 3.02 ms, TI = 900 ms, flip angle = 8° , FOV = 256×224 mm², slice thickness/gap = 1/0 mm, in-plane resolution = 256×224 .

2.4. Preprocessing

The fMRI data were preprocessed by SPM12 (<http://www.fl.ion.ucl.ac.uk/spm>). The first 3 vol were removed to avoid T1 saturation. All functional images were corrected for slice acquisition time and realigned using the first volume as a reference to correct for head movements, and then the T1 anatomical images were co-registered to the functional images. Next, anatomical images were spatially normalized to the Montreal Neurological Institute (MNI) template, and normalization parameters were applied to the functional images. Finally, spatial smoothing with a Gaussian kernel of 6-mm full-width at half-maximum was implemented for univariate analysis.

2.5. Univariate analysis

Univariate analysis was based on a general linear model (GLM). Before analysis, preprocessing data was spatial smoothing with a Gaussian kernel of 6-mm full-width at half-maximum. We first performed a single-subject analysis. A GLM was set up with 9 runs including 3 gaze runs, 3 BM runs, and 3 arrow runs. Every run's regressors consisted of two cue direction conditions (directional and non-directional) and six head motion parameters. All regressors were convolved with the canonical hemodynamic response function. A high-pass filter with a cutoff-frequency of 1/128 Hz was applied to remove low frequency trend. The GLM generates a beta-value for each voxel and regressor, reflecting the impact of each condition on the BOLD signal voxel-wise. Then, a one-sample *t*-test was conducted to test the group-level activation in response to directional versus non-directional conditions for each cue type. Results were corrected for multiple comparisons using threshold-free cluster-enhancement (TFCE) with family-wise error (FWE) at $p < .05$. For visualization, all results were projected on the cortex surface of the BrainNet toolbox (Xia et al., 2013).

2.6. Within-category MVPA

MVPA was conducted on beta maps generated from unsmoothed data (Turner et al., 2012). Following the procedure described by Mumford (2012), single-trial GLMs were generated to estimate the unique beta map for each trial in a run (54 trials in total). Note that the data of the catch trials were discarded. Within each single-trial model, the first regressor modeled the trial of interest, the second regressor modeled all the other trials in that run, six movement regressors obtained in the realigned step within the preprocessing were used to capture head motion, and one constant regressor was also included in the GLM model. Thus, there were a total of 9 regressors in the model. These processes were repeated in each run and for each participant to extract the beta map of 54 trials \times 9 runs (3 gaze runs, 3 BM runs, and 3 arrow runs) from these GLMs for the follow-up MVPA analyses.

In this analysis, a searchlight MVPA was carried out using a support vector machine (SVM) classification as implemented in the CoS-MoMVPA toolbox (Chang and Lin, 2011; Oosterhof et al., 2016). First, the beta-weights were demeaned to ensure that classification was not based on global univariate differences (Reavis et al., 2017). Then, searchlight analyses were executed with 200 voxels across the whole brain (Etzel et al., 2013). For within-category MVPA, we computed classification accuracies using the leave-one-run-out cross-validation method. In each iteration, a classifier was trained to classify directional and non-directional conditions. It should be pointed out that the contrast between directional and non-directional conditions has been used in previous social attention research (Hietanen et al., 2006; Sato et al., 2009) to eliminate the potential influences of perceptual properties of the cues per se. The training of classifier was accomplished by using data from two runs of a specific category (e.g., gaze). Following this, the classifier was tested with data from the remaining run of the same category (e.g., gaze). This procedure was performed in three category cues separately to generate the within-category classification accuracy. For the group-level analysis, a one-sample *t*-test was conducted to compare the decoding accuracies with chance level (50 %), and result maps were also corrected for multiple comparisons using the TFCE-FWE at $p < .001$. For visualization, all results were projected on the cortex surface of the BrainNet toolbox (Xia et al., 2013).

2.7. Regions of interest based on within-category MVPA

To further investigate whether the brain areas found out by the searchlight-based MVPA could decode the attentional effect triggered by other cues, we conducted ROI based within-category MVPA. Based upon the whole-brain MVPA results, we defined 12, 15, and 13 ROIs for the gaze-, BM-, and arrow-mediated attentional effect respectively, and the

peak coordinates were presented in Table 1. In each ROI, all voxels that passed the correction for multiple comparisons (TFCE-FWE corrected $p < .001$) were retained for further analysis. Within each ROI identified from one category, we conducted the ROI-based MVPA to test whether these ROIs could decode the other categories. For example, the ROIs obtained from the whole brain MVPA results of gaze cues were trained and tested on BM cues. It is worth noting that the data of gaze, BM and arrow conditions was acquired in separate runs. For each ROI, the average decoding accuracy was calculated and tested on the group level against the chance level using one-sample *t*-tests. All results were corrected for multiple comparisons using FDR correction at $p < .001$.

2.8. Cross-category multi-voxel pattern analysis

Cross-category MVPA was similar to within-category MVPA except that the classifier was first trained using the data from 3 runs of one category (e.g., gaze) and subsequently tested on its accuracy at classifying the data from 3 runs of the other category (e.g., BM). The reverse decoding was also performed (e.g., first trained on BM and then tested on gaze). The average two-way cross-category classification accuracy was then calculated for each voxel. We repeated such cross-category classification analyses for three combinations of cue types (i.e., gaze-BM, gaze-arrow, BM-arrow) in a pairwise fashion. These analyses were

Table 1
ROI coordinates (in MNI space).

ROI	Hemisphere	BA	x	y	z	T-value
<i>Gaze</i>						
pSTS	R	21	48	-38	4	15.93
Hippocampus	R	37	36	-32	-6	15.84
Lingual	R	18	14	-60	4	20.56
Precuneus	L	23	-10	-58	32	17.21
PCC	R	23	16	-26	38	17.6
Precentral	L	6	-40	-4	44	16.76
	R	6	56	8	38	16.02
Postcentral	L	5	-18	-46	74	16.84
IFG	R	11	24	32	-14	18.55
MFG	L	44	-34	12	30	22.28
	R	9	28	24	46	20.53
SFG	R	9	10	46	42	14.64
<i>BM</i>						
aSTS	R	20	52	2	-22	18.64
pSTG	L	22	-60	-20	6	17.74
Lingual	R	19	22	-62	4	15.63
Cuneus	L	18	-12	-76	30	15.81
	R	19	16	-80	34	15.12
Precuneus	L	17	-22	-56	14	17.31
	R	5	4	-40	58	17.87
IPL	R	40	38	-52	46	15.20
Precentral	L	3	-42	-22	42	18.46
IFG	L	6	-50	4	14	18.67
	R	45	48	36	4	19.73
Insula	R	48	30	-2	16	20.71
ACC	R	32	12	30	24	18.75
MFG	R	6	16	-10	56	18.37
SFG	L	8	-12	24	56	21.86
<i>Arrow</i>						
Hippocampus	L	20	-30	-28	-10	15.44
MTG	L	37	-46	-54	2	16.47
	R	21	46	-54	10	18.72
Cuneus	R	18	10	-74	32	16.78
MOG	L	18	-18	-86	10	20.72
	R	18	22	-94	6	20.91
IPL	L	40	-42	-52	38	25.04
Precuneus	L	5	-4	-52	48	19.45
Posctentral	L	2	-24	-42	64	19.72
IFG	L	48	-44	16	10	19.03
MFG	L	47	-40	38	-4	19.46
	R	44	54	18	36	17.77
ACC	L	32	-12	32	26	16.58

BA, Brodmann's area; R, right; L, left; All results have been corrected for multiple comparisons using TFCE-FWE at $p < .001$.

performed separately for each ROI, and also whole-brain voxels with searchlight analysis. For ROIs, 6-mm spheres were created around these peak coordinates (Table 1) to create the spherical ROIs. For ROI analysis, the classification performance for each participant was averaged across all voxels and the resulting accuracy was entered into a one-sample *t*-test. All results were corrected for multiple comparisons using FDR correction at $p < .001$. For whole-brain analysis, the group-level one-sample *t*-test was conducted to compare the decoding accuracies with chance level (50 %), and result maps were also corrected for multiple comparisons using the TFCE-FWE at $p < .001$. For visualization, all results were projected on the cortex surface of the BrainNet toolbox (Xia et al., 2013).

3. Results

3.1. Behavioral performance

Participants performed the gaze, BM and arrow cueing tasks (Fig. 1, see Materials and Methods for more details) during fMRI scanner. For these three tasks, trials with incorrect responses and reaction times (RTs) beyond 2 standard deviations above or below the mean were excluded from the analyses. The percentage of trials excluded from the analyses was 3.67 % in the gaze cueing task, 3.73 % in the BM cueing task, and 2.94 % in the arrow cueing task. As expected, non-predictive gaze cues could trigger a significant reflexive attentional orienting effect with faster RT for congruent trials as compared to incongruent trials (423 ms vs. 435 ms; $t(20) = -3.24$, $p = .012$, corrected, 95 % Confidence Interval (CI) for the mean difference = $[-20, -4]$, $d = 0.71$, Fig. 2). Similarly, there was a significant attentional effect associated with BM cues (436 ms vs. 442 ms; $t(20) = -2.86$, $p = .030$, corrected, 95 % CI for the mean difference = $[-10, -2]$, $d = 0.62$, Fig. 2). In other words, robust and consistent attentional orienting effects were observed with both types of social cues, replicating previous findings (Driver et al., 1999; Friesen and Kingstone, 1998; Ji et al., 2020; Liu et al., 2021; Shi et al., 2010). Moreover, non-social cues (i.e., arrows) could also induce an analogous attentional effect, (428 ms vs. 442 ms; $t(20) = -3.02$, $p = .021$, corrected, 95 % CI for the mean difference = $[-23, -4]$, $d = 0.66$, Fig. 2), consistent with prior research (Friesen et al., 2004; Tipples, 2002). To directly compare the magnitudes of the attentional effects among these three types of cues, the attentional effect triggered by each type of cue was normalized using the difference in the mean RT obtained under the

incongruent condition versus that under the congruent condition divided by their sum ($(RT_{\text{incongruent}} - RT_{\text{congruent}}) / (RT_{\text{incongruent}} + RT_{\text{congruent}})$). A subsequent one-way repeated measures ANOVA on this normalized attentional effect revealed no significant main effect of cue type ($F(2, 40) = 1.51$, $p = 0.23$, $\eta_p^2 = 0.07$), demonstrating that social and non-social cues elicited comparable attentional orienting effects. The behavioral performance for neutral trials is presented in the supplementary materials.

3.2. Univariate analysis of attentional effects

The contrast between directional and non-directional conditions was examined for each type of central cues to identify the underlying neural mechanisms of the attentional effects. The results revealed that, compared to non-directional cues, directional gaze cues significantly activated the occipital cortex (i.e., bilateral middle occipital gyrus (MOG), right superior occipital gyrus (SOG)), temporal cortex (i.e., bilateral fusiform gyrus (FG), bilateral middle temporal gyrus (MTG), parietal cortex (left superior parietal lobule (SPL), left postcentral), and left middle frontal gyrus (MFG), $p < .05$, TFCE-FWE correction; Fig. 3A). Note that these brain regions, such as the left postcentral and left MFG, have been previously implicated in gaze cueing effect (Hietanen et al., 2006; Joseph et al., 2015). Regarding the BM-mediated attentional effect, results revealed the involvement of the occipital-temporal areas (i.e., bilateral MOG, bilateral FG, bilateral MTG, bilateral STG, bilateral inferior temporal gyrus (ITG)), parietal areas (i.e., bilateral postcentral, left precentral, bilateral SPL, bilateral inferior parietal lobule (IPL), right precuneus), and frontal cortices (i.e., left MFG, left inferior frontal gyrus (IFG), left supplementary motor area (SMA), and left superior frontal gyrus (SFG), $p < .05$, TFCE-FWE correction; Fig. 3B). A part of these brain regions, such as STG, ITG, MTG and IFG, was also found to be involved in BM processing (Chang et al., 2018; Pavlova, 2012; Zillekens et al., 2019). The arrow-mediated attentional effect activated relatively smaller brain areas in the occipital cortex (i.e., bilateral MOG, bilateral inferior occipital gyrus (IOG)) and parietal lobe (i.e., bilateral SPL, bilateral IPL, and left precentral, $p < .05$, TFCE-FWE correction; Fig. 3C). These findings align with previous studies (Engell et al., 2010; Sato et al., 2009), further supporting the consistency of our results. Furthermore, the results indicated that the bilateral FG, bilateral MTG, left SFG, left MFG and some occipital areas (e.g., bilateral IOG and bilateral MOG) were commonly involved in both BM- and gaze-mediated attentional effects ($p < .05$, TFCE-FWE correction; Fig. 3D). Notably, the overlapping brain regions did not encompass the STS or STG. It should be pointed out that previous univariate studies examining the involvement of the right STS/STG in gaze-mediated attentional effect have also yielded conflicting results (Kingstone et al., 2004; Narganes-Pineda et al., 2023). Although some studies have reported that gaze-mediated attentional effect recruited the right STS (Battaglia et al., 2022; Sato et al., 2009; Uono et al., 2014), others have found no evidence supporting its engagement in such attentional effect induced by gaze cue (Engell et al., 2010; Hietanen et al., 2006). This discrepancy may be attributed to several factors, such as variations in task paradigms and the limited sensitivity of univariate analyses. The utilization of MVPA, a more sensitive analysis approach (Norman et al., 2006; Peelen and Downing, 2007), might help us to resolve prior discrepancies in univariate studies.

3.3. Within-category MVPA results

For gaze cues, the whole-brain analysis indicated that the classification accuracy of directional and non-directional cues was above chance in the right pSTS. In addition, the occipital lobe (i.e., right lingual), and parietal lobe (i.e., left precuneus, left postcentral, bilateral precentral, right posterior cingulate cortex (PCC)), as well as frontal lobe (i.e., right IFG, bilateral MFG, right SFG) showed higher accuracy than chance level (Fig. 4A). We further investigated the classification

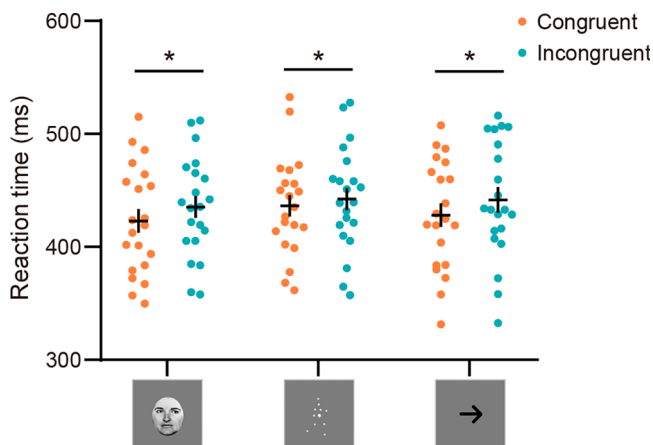


Fig. 2. Mean reaction times in congruent and incongruent trials for three types of central cues. Horizontal black lines show the group-level mean reaction times and vertical error bars show the standard errors of the means. The orange and green dots indicate individual participants' mean reaction times in the congruent and incongruent conditions, respectively. Asterisk indicates statistically significant differences between the congruent and incongruent conditions ($p < .05$, Bonferroni corrected for multiple comparisons).

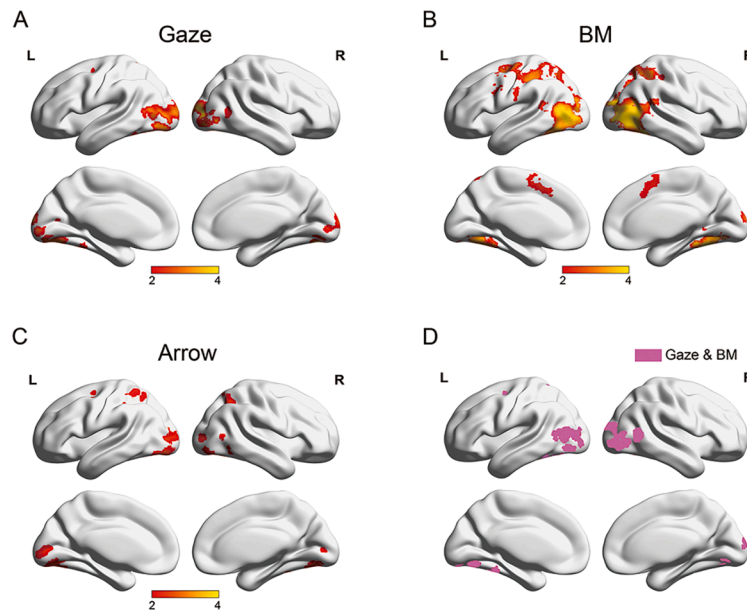


Fig. 3. Univariate results for the attention effect mediated by three types of cues. A shows the brain regions that are activated by the gaze-mediated attentional effect. B shows the brain regions involved in the BM-mediated attentional effect. C displays the brain regions involved in the arrow-mediated attentional effect. D displays the intersection of brain areas involved in the attentional effect mediated by gaze and BM cues, excluding the brain areas associated with the arrow-mediated attentional effect. Results were corrected using TFCE-FWE at $p < .05$.

accuracy of directional and non-directional conditions by using these brain areas as regions of interest (ROIs) to examine whether the brain areas identified from gaze-mediated attention effect might decode the BM- or arrow-mediated attention effect. Results showed that the classification accuracy was higher than chance in the right pSTS and right SFG for BM-mediated attention effect ($p < .001$, false discovery rate (FDR) corrected, Fig. 4B). However, the right pSTS could not decode the directional and non-directional conditions of arrow cues ($p > .05$, FDR corrected). Unlike the right pSTS, the right SFG could decode arrow-mediated attentional orienting ($p = .001$, FDR corrected). Taken together, these results revealed that the right pSTS might also be the critical brain area subserving the attentional effects mediated by gaze and BM but not arrow cues.

For BM cues, the whole-brain analysis indicated that the classification of directional and non-directional conditions was significantly above chance level in the right aSTS and left pSTG. In addition, the occipital lobe (i.e., right lingual, and bilateral cuneus), parietal lobe (i.e., bilateral precuneus, right IPL, and left precentral), as well as frontal lobe (i.e., bilateral IFG, right insula, right anterior cingulate cortex (ACC), right MFG, and left SFG), showed decoding accuracy higher than chance level (Fig. 4C). These results indicate that the encoding of BM-mediated attentional effect involved a broad range of brain areas. Moreover, using these brain areas as ROIs, the classification accuracy of directional and non-directional conditions in gaze and arrow cues was also investigated. Results showed that the classification accuracy was significantly higher than chance in the right aSTS, right IPL, and left precentral for gaze-mediated attention effect ($p < .001$, FDR corrected, Fig. 4D). Notably, the right aSTS was not able to decode arrow-mediated attentional effect ($p > .05$, FDR corrected). Distinct from the right aSTS, the right IPL and left precentral also demonstrated significant ability to classify the directional and non-directional conditions of arrow cues ($p < .001$, FDR corrected, Fig. 4D), suggesting that these areas were not exclusively tuned to BM- and gaze-mediated attentional effects. These findings provided evidence that right aSTS might be the specialized brain area responsible for encoding the attention effects triggered by social but not non-social cues.

Furthermore, we also investigated the whole-brain classification accuracy of directional and non-directional conditions for arrow cues.

The results showed that the subcortical area (i.e., left hippocampus), occipital lobe (i.e., right cuneus, bilateral MOG), temporal lobe (i.e., bilateral MTG), left parietal lobe (i.e., IPL, precuneus, postcentral), frontal lobe (i.e., left IFG, bilateral MFG, left ACC) could decode arrow-mediated attentional effect (Fig. 4E). This suggests distributed neural processing of attentional effects related to arrow cues across various brain regions. Using these brain areas as ROIs, we found that the classification accuracy was higher than chance in the left MTG and left postcentral for BM and gaze cues ($p < .001$, FDR corrected, Fig. 4F).

3.4. Cross-category MVPA results

The within-category MVPA results delineated the underlying neural substrates for the attentional effects mediated by the three types of cues and showed that the right aSTS and the right pSTS are potentially the shared brain areas for gaze- and BM-mediated attentional orienting effects. Here, we implemented the cross-category MVPA with ROI-based and searchlight-based analyses across three pairs (i.e., gaze-BM, gaze-arrow, and BM-arrow) to further identify whether there exists a shared neural mechanism dedicated to the attentional orienting effects mediated by social cues (i.e., gaze and BM) but not non-social cue (i.e., arrow). The cross-category MVPA can verify whether the information encoded in spatial patterns is consistent across different categories or conditions (Yang et al., 2012), providing novel quantitative evidence for theories that posit a shared mechanism.

Firstly, we tested whether the right aSTS and the right pSTS (Fig. 5A) implicated in social attention from within-category MVPA can also significantly cross-category decode directional and non-directional condition in the pair of gaze-BM. Results showed that both ROIs could significantly decode the pair of gaze-BM ($p < .001$, FDR-correction, Fig. 5B), but not significantly decode the pairs of gaze-arrow or BM-arrow. These results indicated that both the right aSTS and the right pSTS were involved in the attentional effects mediated by social cues but not non-social cues. This finding resonates well with a prior study demonstrating that the aSTS codes the direction of another's attention regardless of how this information is conveyed (Carlin et al., 2011).

Furthermore, the whole-brain searchlight analysis with 200 voxels was applied to the three pairs. For the pair of gaze-BM, results showed

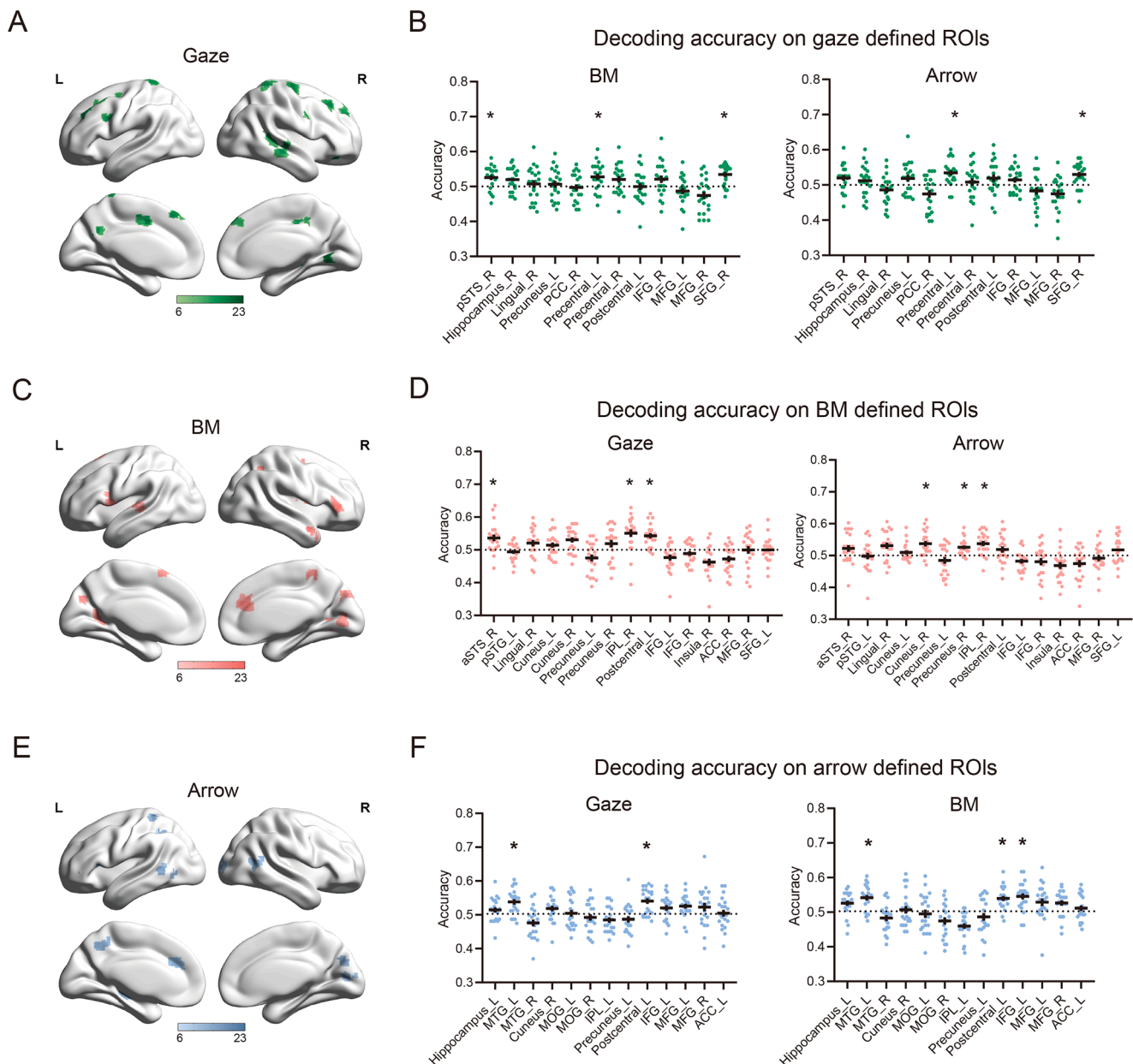


Fig. 4. Within-category MVPA results for the attentional effects mediated by three types of cues. A, C, and E display the results of the searchlight MVPA for gaze-, BM-, and arrow-mediated attention effect, respectively. Statistical maps have been corrected for multiple comparisons using threshold-free cluster-enhancement (TFCE) with family-wise error (FWE) at $p < .001$. B, D, and F show the ROI-based MVPA results. B shows the ROIs defined by gaze (A). The left panel and right panel are corresponding to the classifications trained and tested on BM and arrow cues, respectively. D shows the ROIs defined by BM (C). The left panel and right panel are corresponding to the classifications trained and tested on gaze and arrow cues, respectively. F shows the ROIs defined by arrow (E), the left panel and right panel are corresponding to the classifications trained and tested on gaze and BM cues, respectively. Asterisk indicates that the classification accuracy is significantly above chance ($p < .001$, FDR correction).

that above-chance classification was possible through mostly the ventral part of the right temporal cortex (i.e., right MTG, aSTG, pSTG, and fusiform gyrus), the frontal cortex (i.e., precuneus, ACC, SFG, SMA in the right hemisphere, left IFG, and bilateral MFG), and left precentral lobe (directional vs. non-directional, $p < .001$, TFCE-FWE corrected, Fig. 6A). For the pair of gaze-arrow, results showed that above-chance classification was mainly located in the frontal (i.e., bilateral insula, bilateral SFG, and right ACC), parietal cortex (i.e., left IPL, left precentral, and right postcentral), and right MTG ($p < .001$, TFCE-FWE corrected, Fig. 6B). For the pair of BM-arrow, results showed that frontal (i.e., insula, SFG, MFG in the bilateral hemispheres, and right ACC) and parietal cortex (i.e., left postcentral, bilateral precentral) could significantly decode the BM- and arrow-mediated attentional effects ($p < .001$,

TFCE-FWE corrected, Fig. 6C).

We went further to identify the specialized neural mechanism underlying social attention by comparing the results of cross-category decoding for gaze-BM, gaze-arrow, and BM-arrow. Both ROI-based and whole-brain MVPA results identified that the right STS/STG as the critical regions that could specifically decode social but not non-social attentional effects. These results are in line with previous neuroimaging studies demonstrating a pivotal role of the STS for gaze cueing effect (Kingstone et al., 2004; Uono et al., 2014; Vaidya et al., 2011). Moreover, we found that the right insula, right SFG, right MFG, and left precentral could decode the attentional orienting effects across social and non-social cues, reflecting a general attention network (Fig. 7). Although the current design varies between the BM and eye gaze cues,

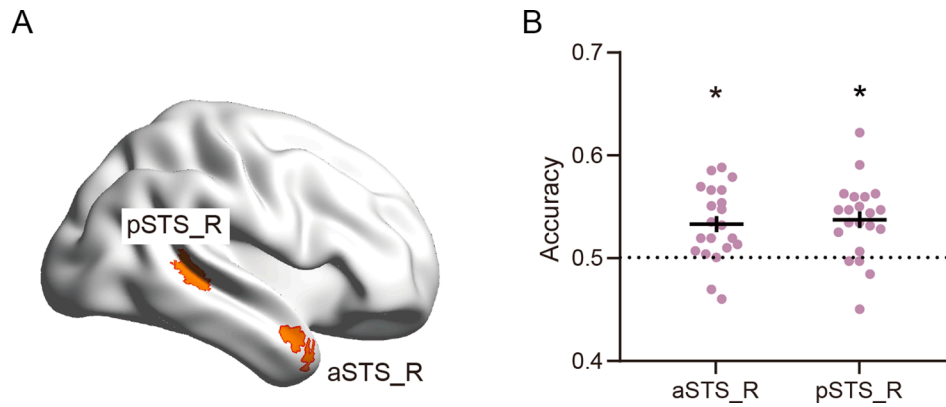


Fig. 5. ROI-based cross-category MVPA reveals significant decoding accuracy in the pair of gaze-BM. (A) The locations of the ROIs (i.e., right aSTS and right pSTS). (B) The classification results for gaze-BM within the separate ROIs. Scatter plots represent the decoding accuracy for individual participants. The horizontal black lines represent the group-level mean decoding accuracies and the vertical error bars display the standard errors of the means. Asterisk indicates that the classification accuracy is significantly above chance ($p < .001$, FDR correction).

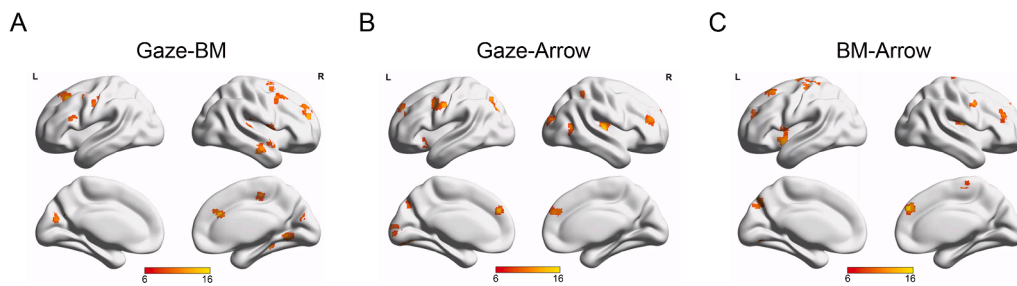


Fig. 6. Results of the searchlight-based cross-category classification for three pairs. (A), (B), and (C) represent the statistical maps for the gaze-BM, gaze-arrow, and BM-arrow pairs, separately. These results were corrected by TFCE-FWE with $p < .001$.

we have found common brain areas for the attention effects mediated by both cues. Thus, the main findings of our study cannot be explained by the stimuli presentation procedures. However, the different presentation procedures for eye gaze and BM cues might indeed interfere with discovering more shared brain areas between the two. Future studies could consider designing the presentation procedure for BM cues to be consistent with that of gaze cues.

4. Discussion

Humans are endowed with an exceptional ability for coordinating attention with others in reference to an event or an object in the environment (Nummenmaa and Calder, 2009). In the current study, we implemented the fMRI technique in conjunction with a modified central cueing paradigm to elucidate the specialized brain mechanisms underlying this social attention behavior. Using fMRI-based MVPA, we found that BM-mediated attentional orienting could be decoded from neural activity in a wide range of brain areas including the right aSTS, right pSTS, and left pSTG, part of the occipital lobe (i.e., bilateral cuneus and right lingual), and right frontal-parietal network (e.g., IPL, IFG, and MFG). Moreover, the right aSTS and pSTS could also decode attentional orienting triggered by another type of social (i.e., gaze) but not non-social (i.e., arrow) cues. More importantly, cross-category MVPA revealed that social attention could be decoded across gaze and BM cues in the right STS/STG, providing direct evidence for the existence of shared brain areas responsible for social attention evoked by different types of social cues (gaze and BM).

To the best of our knowledge, our study represents the first investigation into the neural mechanisms underlying attentional effects mediated by BM cues. Our results of MVPA demonstrated that the right STS exhibited significant decoding of BM-mediated attentional orienting. The right STS has been linked to the processing of BM direction

(Grèzes et al., 2013; Wang et al., 2023), as well as the intentions conveyed by social cues (Allison et al., 2000; Pelphrey et al., 2004). Moreover, BM-mediated attentional orienting could also be encoded in an extensive neural network that included the ventral (i.e., MFG, Insula, ACC, and IPL in the right hemisphere, and bilateral IFG) and dorsal (i.e., left SFG and left precentral) cortical areas. Most of these cortices have been ascribed functions in various aspects of attentional processing (Hietanen et al., 2006; Joseph et al., 2015; Kingstone et al., 2004). In particular, the MFG, IFG, IPL and Insular, key regions of the ventral attention network, have been implicated in exogenous attention (Fiebelkorn and Kastner, 2020). The significant decoding of BM-mediated attentional orienting in these ventral areas therefore supports the notion that BM cues can direct attention reflexively (Shi et al., 2010; Wang et al., 2014).

The brain mechanisms underlying social attention have already been widely investigated by adopting eye gaze as a central cue in previous studies, yet the findings are mixed (Greene et al., 2009; Hietanen et al., 2006; Joseph et al., 2015; Koike et al., 2019; Lee et al., 2010). While several neuroimaging studies have reported that gaze-mediated orienting recruits the ventral attention network (e.g., IFG, IPL, and MFG; Engell et al., 2010; Sato et al., 2016), some others found the involvement of the dorsal attention network (e.g., SFG, and precentral) in modulating the attentional effect induced by gaze (Hietanen et al., 2006; Joseph et al., 2015). Several factors have been identified to account for these discrepant findings, such as low-level perceptual properties of gaze cues, analytical method and so forth (Birmingham and Kingstone, 2009; Engell et al., 2010; Gregory and Jackson, 2021; Joseph et al., 2015). In the present study, we employed MVPA, a more sensitive and effective method for studying brain representations (Peelen et al., 2006), and demonstrated that gaze-mediated attentional effect could be decoded in the right STS, as well as widespread brain regions within both the ventral attention network (Callejas et al., 2014; Sato et al., 2009;

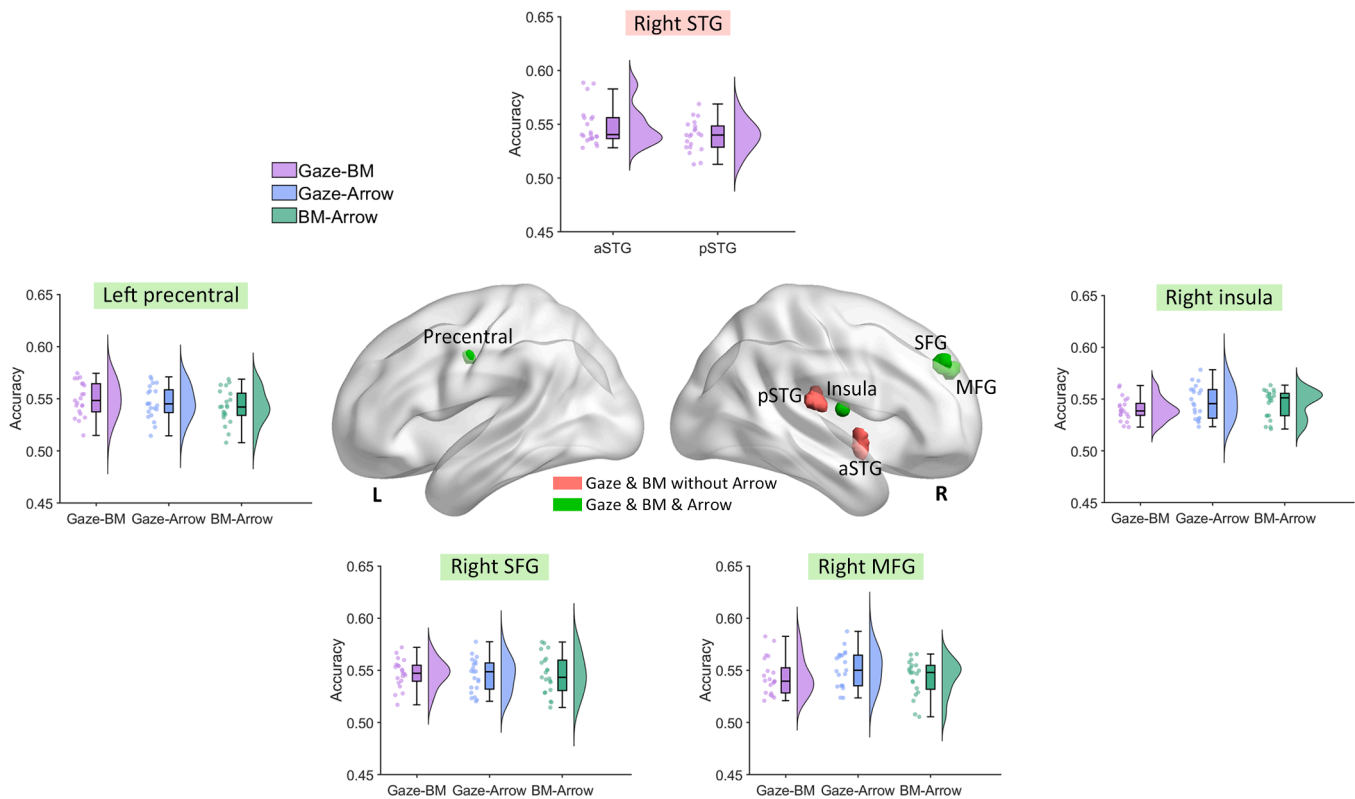


Fig. 7. The overlapping brain areas and decoding accuracy of cross-category classification across three pairs. The right aSTG and right pSTG were identified as significant regions in the statistical map of gaze-BM, excluding the gaze-arrow and BM-arrow pairs, which means both areas are specialized for social attention effects. The right insula, right SFG, right MFG, and left precentral were identified as overlapping regions in the searchlight MVPA results for all three pairs with a lower threshold at $p < 10^{-6}$ (uncorrected). Scatter plots depict the decoding accuracy for individual participants in each brain area and each pair. Box plots represent the group-level mean decoding accuracy, and vertical error bars indicate the standard errors of the means. Violin plots display the distribution of the decoding accuracy. Lavender, blue, and green dots correspond to the cross-category MVPA results for the gaze-BM, gaze-arrow, and BM-arrow pairs, respectively.

Schilbach et al., 2011) and the dorsal attention network (Hietanen et al., 2006; Joseph et al., 2015). Although BM cues are very different from gaze cues in terms of perceptual properties, the attentional effects triggered by these two types of social cues engage overlapping brain regions, including the pSTS, aSTS, IPL, and SFG in the right hemisphere and left precentral. More importantly, cross-category MVPA analyses revealed that the right temporal cortex (i.e., MTG, aSTG, pSTG, and FG), frontal cortex (i.e., left IFG, right precuneus, right ACC, right SFG, right SMA, and bilateral MFG), and left precentral lobe exhibited significant decoding of social attention across gaze and BM cues. Therefore, the inclusion of BM cues in our investigation ameliorated the concern regarding the confounding factor of perceptual properties and enhanced our understanding of the brain mechanisms underlying social attention. Taken together, our findings suggest that common brain regions might be involved in subserving the attentional orienting elicited by different types of social cues, providing evidence for the existence of a general system supporting social attention in the human brain. However, there is also a possibility that the brain areas for social attention might be engaged in social cue perception prior to the involvement of attention. This limitation arises because the temporal resolution of fMRI is insufficient to separate the stages of cue perception and cue mediated attention. Despite the use of stimuli with significantly varied physical features, the potential for a cue categorical effect has not been completely excluded. Therefore, future investigations may benefit from implementing techniques such as magnetoencephalography (MEG), which offers high temporal resolution and source accuracy, thereby helping to distinguish perception from attentional processes.

Considering the evidence showing that non-social cues like arrows can provoke automatic attentional shifts similarly (Ristic and Kingstone, 2006; Tipples, 2002), our study also places a significant emphasis on

elucidating the neural distinction between social and non-social attention. To date, existing behavioral and neuroimaging studies often directly contrasted social and non-social attention by employing eye gaze and arrow as the central cues, yet have yielded inconsistent results (Hietanen et al., 2006; Joseph et al., 2015; Kingstone et al., 2004; Sato et al., 2009). Several neuroimaging studies have reported distinct attentional networks activated by gaze and arrow cues (Engell et al., 2010; Lockhofen et al., 2014), exemplified by one fMRI study accentuating the role of the ventral attention network, particularly the TPJ implicated in social cognition (Bzdok et al., 2013; Dugué et al., 2018; Schuwerk et al., 2017), in gaze-evoked but not arrow-prompted orienting (Joseph et al., 2015). Conversely, some other research indicated overlapping neural mechanisms for these two types of attentional orienting (Greene et al., 2009; Sato et al., 2009; Uono et al., 2014). The lack of a unified understanding motivates our investigation, which employs cross-decoding MVPA to explore this dichotomy. Our noteworthy results disclosed that the right STS/STG could decode attentional orienting across different social (gaze and BM), but not non-social (arrow) cues. This finding provided support for the unique nature of social attention and implied that the right STS/STG may play a role as a candidate hub specialized for social attention. Furthermore, we also identified some areas specialized for arrow-mediated attentional effect, such as the MOG, IPL and ACC, which is consistent with findings from prior studies on arrow cueing (Engell et al., 2010; Salera et al., 2023). Importantly, we found a widespread attentional network encompassing the MFG, SFG, insula, and precentral gyrus, capable of decoding both social and non-social attentional effects. Collectively, we speculated that there are two systems for social and non-social attention, each with its own specialized brain regions (STS/STG for social, MOG, IPL for non-social) as well as some overlapping areas (i.e., MFG, SFG, insula, and

precentral). Additionally, future studies could utilize transcranial magnetic stimulation (TMS) to further clarify the distinctions between social and non-social attentional systems.

Notably, the emergence of general representations (right MFG, and right insula, right SFG, and left precentral) for social and non-social attention raises questions about their origination. One hypothesis is that both gaze and arrow stimuli, as behaviorally relevant directional cues, can elicit a new form of spatial attention (i.e., automated symbolic orienting) that occurs as a result of long-term learning of cue-target contingencies in the environment (Ristic and Kingstone, 2012). This notion has been supported by our prior behavioral genetic study demonstrating that the interplay between gaze and arrow cueing effects is largely shaped by environmental factors, in sharp contrast to the covariation between gaze and BM cueing effects that is mostly explained by shared genetic effects (Wang et al., 2020). Our findings, coupled with the former evidence, implied that social attention not only relies on an innate neural mechanism (i.e., right STS) but also depends upon an acquired, more general attentional neural system (i.e., MFG, insula, and SFG in the right hemisphere and left precentral) shared by non-social attention. Taken together, our insights contribute to resolving the conflicting outcomes of past research and enhance our understanding of the neural mechanisms underlying social and non-social attentional effects.

In conclusion, the current study clearly demonstrates that the right STS/STG could encode social attention across gaze and BM cues, providing neural evidence for the existence of shared brain areas responsible for these two different types of social attention behaviors. Conversely, these regions could not decode attentional orienting across social and non-social cues, suggesting that the brain mechanisms involved in social attention may be distinct from those involved in non-social attention. Collectively, these findings support the notion of a dedicated social attention module in the human brain, highlighting the right STS/STG as the key neural locus for social attention.

CRediT authorship contribution statement

Ruidi Wang: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Tian Yuan:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Li Wang:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Yi Jiang:** Writing – review & editing, Visualization, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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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.2024.120889](https://doi.org/10.1016/j.neuroimage.2024.120889).

Data availability

Anonymized data and the stimuli associated with this work are available at <http://ir.psych.ac.cn/handle/311026/47041>.

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