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Research report

Neural representation of animacy in the early visual areas: A functional MRI study

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ARTICLE INFO

Article history: Received 21 October 2008 Received in revised form 25 March 2009 Accepted 25 March 2009 Available online 1 April 2009

Keywords: Animacy fMRI Lateral occipital complex Object identification Ventral visual pathway Visual motion

ABSTRACT

Animacy helps to identify objects as living entities. To test the hypothesis that the perception of animacy via visual motion cues is represented in the same ventral visual pathways associated with living object identification through static visual information processing, 28 normal volunteers underwent functional MRI whilst tracking the movements of a self-propelling object. The target movement was held constant between conditions, whilst the animacy was externally manipulated by the presence of "chasers", from which the target was perceived to be escaping, and by "obstacles", which were static geometric objects with which the target avoided collision. The perception of target animacy was most powerfully induced by chasers, and a proximity effect was more prominently produced by obstacles. Animacy as induced by a chaser was associated with effects in the bilateral occipital poles (OPs) and the left inferior temporal gyrus to the lateral occipital complex (LOC). The LOC showed a stronger animacy effect, relative to the proximity effect, than the OPs. The effective connectivity between the LOC and the OPs was bi-directionally enhanced by the chasers. These findings suggest that both the LOC and the OPs play important roles in the identification of animated entities through the integration of information about the relationships between objects encoded in retinotopic coordinates.

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1. Introduction

For living beings, including humans, the identification of other animate entities is essential for survival. Animacy is perceived by way of visual motion cues that are independent of form. One important visual cue of animacy is the presence of self-propelled motion, which is motion that cannot be explained by simple physical rules such as gravity, collision, and magnetic forces (the Newtonian violation hypothesis; [3]). Additionally, as "approach" and "avoidance" are common characteristics of all animals [2], the percept of animacy is also strongly related to an organism's goals and desires. Recent psychophysical experiments have shown that goal-directed movement, which is a type of autonomous movement in which the object's movement is contingently directed towards or away from another object, state, or location, is a commensurate standard by which people identify novel entities as living things [40].

For humans, in particular, the identification of goals and desires is fundamental for mindreading [2] or mentalizing [20], which describe the ability to infer the mental states of others. Heider and Simmel [29] demonstrated that some geometrical objects' movements induce the impression of animacy, even when stimuli lack concrete animate features. The subjects spontaneously interpreted moving shapes as agents driven by internal mental states.

Based on these findings, Baron-Cohen [2] postulated the existence of a psychological mechanism, termed an intention detector (ID): "a perceptual device that interprets motion stimuli in terms of the primitive volitional mental states of goal and desire". Baron-Cohen also considered another perceptual device, the theory-of-mind mechanism (ToMM). This includes "a way of representing the set of epistemic mental states" (including pretending, thinking, knowing, believing, imagining, and so on) and "a way of tying together these mental states into a coherent understanding of how mental states and actions are related". In the case of face-to-face communication, these two modules, and the additional modules of the eye-direction detector (EDD) and shared attention mechanism (SAM), support mindreading mechanisms through shared gaze or joint attention. Thus, according to the model of

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^{0361-9230/\$ -} see front matter © 2009 Elsevier Inc. All rights reserved. doi:10.1016/j.brainresbull.2009.03.007

Baron-Cohen [2], Heider and Simmel had evoked mentalization in participants, who attributed visual stimuli with mental states by means of the ID and the ToMM.

Using similar stimuli to Heider and Simmel, recent neuroimaging studies showed that more complex movements of the observed geometrical objects produced greater activation of the lateral fusiform gyrus and the posterior superior temporal sulcus (pSTS) [8,36]. Castelli et al. presented "scripts" for ToM sequences that "involved the two triangles persuading, bluffing, mocking and surprising one another". These ToM scripts activated the medial prefrontal cortex, the temporal pole, and the temporoparietal junction (TPJ), all of which effects were attributed to the mentalizing process [20]. Additionally, they reported activation in the fusiform gyrus and the occipital pole (OP). Castelli et al. [8] suggested that this visual cortical activation was due either to the varying complexity of the stimuli or to the attention towards local processing relevant to the attribution of animacy. However, according to the mindreading model of Baron-Cohen, another interpretation can be proposed: it is possible that regions early in the visual stream respond to visual-kinetic information about intention to act [8], which contributes to the perception of animacy. This supports the hypothesis that the neural substrates of ID are distinct from those of ToMM. Furthermore, Castelli et al. found that "scripts" for less complicated goal-directed sequences, such as those that "involved the two triangles dancing together, one chasing, one imitating, and one leading the other", activated the OP [8]. This finding suggests that the animacy percept might depend on access to visual information about subtle changes in the dynamic relationship between objects. Developmentally, the animacy percept emerges at an extremely early age (around 3-4 months) [21], which is long before the emergence of the ToM, as tested with a false belief task (at around 4-5 years of age) [20]. This implies that the neural substrates of the animacy percept constitute a module that is independent of the "mentalizing" network.

The posterior part of the inferior and middle temporal sulcus/gyrus and the fusiform gyrus are associated with the conceptual representation of objects such as faces (the fusiform face area or FFA) and body parts (the extrastriate body area or EBA). Recent studies have suggested the existence of an animate-object-specific area in the lateral fusiform gyrus and the STS [9,12,31]. The bilateral fusiform gyrus and the middle temporal gyrus (MTG)/STS responded more strongly to animate objects (that is, bodies, faces, mammals, birds, fish, insects, spiders, and reptiles) than to inanimate objects (that is, tools, crystals, musical instruments, cars, weapons, prepared foods, clothes, chairs, and fruits and vegetables). These regions partially overlap with the EBA and the FFA in both the left and right hemispheres [12]. Furthermore, Chao et al. [9] reported that activity of the inferior occipital gyrus (IOG) occurred in response to photographs of animals. As this activation was also found in response to the written names of animals, the authors speculated that the identification of animated objects requires the top-down modulation of the early visual processing stream, possibly from the ventral temporal region. However, these previous studies have been concerned with object identification via morphological and/or semantic cues. Motion is no less ambiguous in terms of ontological category than are the static features of objects; thus, we must use both resources to achieve the correct identification of novel cases of animate and inanimate objects [21]. However, it is not yet known how animated object identification via motion cues is represented in the visual cortex.

The purpose of the present study was to investigate the neural substrates of animate object identification through motion cues, using functional magnetic resonance imaging (fMRI). Our hypotheses were as follows: first, that the neuronal activity of the animate-object-specific areas in the posterior temporal gyrus and the IOG covary with the degree of animacy perception even without a top-down process of mentalizing; and second, that animated object identification via motion cues is represented by the coactivation of the ventral temporal region with the early visual cortices. Animacy was manipulated by varying the extent to which the target's movements were perceived as goal-directed. Specifically, we used "chaser" objects that the target object contingently directed its movement away from, and "obstacle" objects with which the target avoided collision. Visual stimuli comprising a self-propelled target object, together with the presence of a chaser object, were hypothesized to evoke a stronger percept of animacy than the same stimuli lacking any chase-like behavior. However, chasing movements are usually accompanied by increased object proximity, and might confound efforts to isolate the effects of the chaser alone. We therefore introduced "obstacles" into the visual displays, to evaluate any possible proximity effect. Obstacles are known to be much weaker inducers of animacy [21]. Thus, the percept of target animacy, as well as any proximity effect, can be manipulated by the presence or absence of "chasers" and "obstacles" whilst the properties of the target's motion (including speed) can be held constant. The participant's task was to track the target object at all times. We adopted a visual target tracking task for several reasons. The first was to eliminate the effect of mentalizing or varied attention [44] and thereby to isolate the neural substrates of the ID. The second was to control the amount of eye movements across the conditions. To accomplish this, the target speed was held relatively low (about $3^{\circ}/s$) compared with a previous study in which it was $6-20^{\circ}/s$ [44]. Third, the use of a visual tracking task allowed us to evaluate the proximity effect by varying the number of the objects in the central visual field. We were therefore able to evaluate separately the proximity and animacy effects.

2. Methods

2.1. Subjects



Fig. 1. Four task conditions. The task of the participants was to follow the red disk, and to detect the change in the frame color of the red disk the trajectories of which were identical across the four conditions. The four conditions are characterized by the presence or absence of chase behavior of the blue disk (chase) and obstacles (obstacle), constituting a 2×2 factorial design. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

A total of 28 healthy subjects (13 females; 15 males) participated in the study, with a mean age of 24.1 ± 3.6 years. The subjects were all right-handed according to the Edinburgh handedness inventory [39], and had a normal or corrected-to-



Fig. 2. Characteristics of the task stimuli. (A) The speed of the target red and blue disks in the chaser (CO and CN) and no-chaser (NO and NN) conditions. The red line indicates the speed of the target disk, and the blue and green lines indicate the speed of the blue disk in the chaser and no-chaser conditions. (B) The distance between the target red disk and the blue disk. The blue and green lines indicate the distance in the chaser and no-chaser conditions. (C) Visual field dimensions used to determine the number of visual elements. There are the three obstacles within the red dashed line (diameter, 3.7°). (D) The mean number of visual objects, including both obstacles and the blue disk, for the different conditions. We defined the measuring range as the radius of the red dashed line in (C), and counted the number of visual objects within the reader is referred to the web version of the arritcle.)

normal vision. There was no history of neurological or psychiatric illness in any of the subjects, and none had any neurological deficits. The protocol was approved by the ethical committee of the National Institute for Physiological Sciences, Japan. The experiments were undertaken in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki). Subjects participated in both psychophysical experiments and fMRI.

2.2. Task stimuli

Four computer-generated video-clips of 15 s duration were prepared with Delphi 6.0 (Borland Software Corporation, Austin, TX) implemented on a personal computer (Dell Precision 380; Dell Computer, Round Rock, TX) (Fig. 1). All of the video-clips consisted of two disks, one red and one blue, moving smoothly against a gray rectangular background with a visual angle size of $7.3^{\circ} \times 7.3^{\circ}$ and a viewing distance of approximately 60 cm. The radius of the target red disk was 0.16° and that of the chaser blue disk was 0.25° . The trajectory of the red disk was identical across the four displays. The frame color of the red disk was to follow the target red disk visually at all times and to detect the temporary changes in frame color.

We manipulated the animacy of the target red disk by adding two features: "chaser" objects (C) and "obstacle" objects (O). As a chaser object, the blue disk moved towards the target red disk, which moved away to "escape" from the chaser. Static geometric objects served as obstacles, with which the target avoided collision. Using these features, we generated four experimental conditions: chaser with obstacle (CO), chaser without obstacle (CN), no-chaser with obstacle (NO), and no-chaser without obstacle (NN) (Fig. 1). In the CO condition, the target disk was chased by a blue disk in the presence of four pairs of black rectangles (obstacles). The obstacles were composed of a pair of rectangles (0.33 $^{\circ} \times 0.66^{\circ})$ at a 0.44 $^{\circ}$ interval, which were in a non-overlapping position in the display (Fig. 1). To establish the "chasing" trajectories, an attraction force acting on the blue disk towards the red target disk was set proportional to the square of the distance between the disks. A repulsion force acting on the red target disk, away from the blue disk, was set proportional to the square of the inversion of the separation distance. Repulsion forces repelling both disks from the obstacles were set proportional to the square of the inversion of the distance, so as to avoid collision; thus, no collision occurred. In the NO condition, no attraction or repulsion forces were applied between the disks, and so the target and blue disks moved independently. In this condition, the trajectories of the blue disk were selected such that it did not collide with the target, whilst the trajectory of the target disk was identical to that in the CO condition. The CN and NN conditions were identical to the CO and NO conditions, respectively, with the exception that in the two latter conditions the obstacles were invisible.

The characteristics of the stimuli are summarized in Fig. 2. The average disk speeds were as follows: target red disk=2.79 (standard deviation [SD]=0.50)°/s; blue disk in chaser condition = 2.65 (SD = 0.23)°/s; and blue disk in no-chaser condition = 2.61 (SD = 0.22)°/s. Thus, the target disk was faster than the blue disk (chaser,

p < 0.05; no-chaser, p < 0.05). The blue disk speeds were not significantly different between the chaser and no-chaser conditions (p = 0.26). In the chaser condition, the blue disk was significantly closer to the target disk than in the no-chaser condition (p < 0.001). The proximity effect by means of the number of visual elements (that is, the blue disk and obstacles) was mainly determined by the obstacles: within the circular central visual field with a diameter of 3.7° , the number of elements was 0.03 ± 0.04 (mean \pm SD) in the NN condition, 1.43 ± 0.16 in the NO condition, 0.62 ± 0.14 in the CN condition, and 2.02 ± 0.26 in the CO condition (Fig. 2D).

2.3. Experimental procedure

2.3.1. Psychological measurement

The psychological experiments were done outside the scanner. Subjects observed the animation stimuli (CO, CN, NO, and NN) on an LCD display outside the MRI scanner, before and after the fMRI scans. The viewing distance was approximately 60 cm, and the width and height of the display were 31.0° and 25.8°, respectively. The field size was 14.0° × 14.0°. Each animation was presented nine times. The duration of each animation was 15 s, and the order of conditions was pseudo-randomized. Subjects were required to evaluate the degree of animacy of the target disk using a seven-point scale.

2.3.2. fMRI experiment

During the fMRI experiment, all of the stimuli that were used in the psychological experiment were projected onto a half-transparent screen located behind the head coil by an LCD projector (DLAM200L, Victor, Yokohama, Japan). Subjects viewed the screen via a mirror mounted on the head coil. The viewing distance was approximately 60 cm, and the projected display width and height were 18.9° and 14.2°, respectively. Presentation 0.92 (Neurobehavioral Systems Inc., Albany, CA) on a personal computer (Dimension 9100; Dell Computer, Round Rock, TX) was used to collect and record the responses via an optical button-box (Current Designs Inc., Philadelphia, PA).

The subjects underwent the visual tracking task in the MRI scanner. A block design was employed. Each session consisted of 12 animation conditions and 12 control fixation conditions. Each condition was 15 s in duration, with alternating animation and fixation. The four animation conditions described above (CO, CN, NO, and NN) were repeated three times in a pseudo-random way. In the control fixation condition (FIX), only a static image, in which the target was presented at the centre of the screen, was displayed continuously. The subjects were required to track visually the target disk throughout the session, during both the animation and fixation conditions, and to press a button with the right index finger when the frame color of the disk changed from red to black, which occurred every 4–6 s with a 1 s duration. Each session took 6 min and 12 s, and was repeated three times.

All images were acquired using a 3T MR scanner (Allegra, Siemens, Erlangen, Germany). For functional imaging during the sessions, an interleaved T2*-weighted gradient-echo echo-planar imaging (EPI) procedure was used to produce 44 continuous 3 mm thick transaxial slices covering the entire cerebrum and cerebellum (repetition time [TR]=3000 ms; echo time [TE]=30 ms; flip angle=85°; field of view=192 mm; 64×64 matrix; and voxel dimensions=3.0 mm × 3.0 mm × 3.0 mm). Oblique scanning was used to exclude the eyeballs from the images. To acquire a fine-structural whole-head image, T1-weighted magnetization-prepared rapid-acquisition gradient echo (MP-RAGE) images were also obtained (TR=2500 ms; TE=4.38 ms; flip angle=8°; field of view=230 mm; number of slices per slab=192; and voxel size=0.9 mm × 0.9 mm × 1.0 mm). The total duration of the experiment was approximately 90 min, including the instruction period, the psychological experiments, and the acquisition of the structural and fMRI data.

2.4. Data analysis

2.4.1. Image preprocessing

The first three volumes of each session were eliminated to allow for stabilization of the magnetization, and the remaining 121 volumes per session (a total of 363 volumes) were used for the analysis. The data were preprocessed using SPM5 (revision 748) (Wellcome Trust Centre for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm) implemented in Matlab 2006b (Mathworks, Natick, MA). After realignment for motion correction, all EPI volumes were normalized into the EPI template that was already fitted to a standard stereotaxic space by the Montréal Neurological Institute (MNI), using the affine and non-linear threedimensional transformations. The EPI volumes were spatially smoothed in three dimensions using an 8 mm full-width at half-maximum Gaussian kernel.

2.4.2. Statistical analysis

Statistical analysis was conducted at two levels. At the first level, individual taskrelated activity was evaluated. At the second level, in order to make inferences at a population level, individual data were summarized and incorporated into a random effects model [30].

2.4.2.1. Individual analysis. The signal time-course of each subject, with 363 time points, was modeled with four regressors of interest that accounted for each condition (CO, CN, NO, and NN), and another regressor for the response of the target color-change detection task. These regressors were convolved with a canonical hemodynamic response function. A high-pass filter with a cut-off period of 128 s was applied to eliminate the artifactual low-frequency trend. No proportional scaling was performed; instead, session-specific scaling was applied, in which each volume was divided by session-specific scaling factors that were estimated based on the volume-wise intra-cerebral mean intensity (grand mean scaling). As this scaling rendered the mean global activity 100, the signal change was interpreted as a percent of the global mean [32]. Serial autocorrelation assuming a first-order autoregressive model was estimated from the pooled active voxels with a restricted maximum likelihood (ReML) procedure [18]. The least-square estimation was performed on the filtered and pre-whitened data and design matrix, to give the estimated parameters.

2.4.2.2. Group analysis. The weighted sum of the parameter estimates in the individual analysis constituted "contrast" images, which were used for the second-level (group) analysis [30]. Two-way repeated measures analysis of variance (rmANOVA) at the second level, incorporating chase and obstacle as main effects and their interaction, was conducted using contrast images generated from the estimates for the regressors of CO, CN, NO, and NN for each subject. The resulting set of voxel values for ANOVA comparisons constituted a statistical parametric map (SPM) of the *t* statistic (SPM{*t*}). The statistical threshold was set at *p* < .05 with a false discovery rate (FDR) correction for multiple comparisons [22] at the voxel level, and *p* < .05 corrected at the cluster level [17] for the entire brain. Additionally, the areas that were activated by all conditions (CO, CN, ON, and NN) were depicted by means of conjunction analysis with the conjunction null hypothesis [38] and a statistical threshold of FDR corrected to *p* < .05 at the voxel level.

The contrast [(CO+CN) - (NO+NN)] showed a chase effect in three discrete regions in the OPs bilaterally and the left inferior temporal gyrus (ITG). As the presence of a chaser most strongly induced the animacy percept, we performed further analyses on these regions at different locations. For the blood oxygen level-dependent (BOLD) signal change in the detected regions, we conducted a three-way rmANOVA (location × chase effect × obstacle effect) using SPSS software (SPSS Inc., Chicago, IL). To evaluate the contribution of the proximity effect, calculated on the basis of the stimuli (Fig. 2D) and the animacy effect on a perceptual judgment (Fig. 3), to the activation, we conducted an analysis of covariance (ANCOVA), in which the BOLD signal change of the three regions was modeled by incorporating the normalized (centered to zero mean and scaled to unity) proximity scores and animacy scores a the contribution of the animacy and proximity effect.

2.4.3. Evaluation of effective connectivity using dynamic causal modeling (DCM)

To evaluate the functional relationship between the left OP and the ITG, the effective connectivity was evaluated. Effective connectivity is defined as the influence that one neural system exerts over another [19]. DCM is one approach for the analysis of effective connectivity using experimentally designed inputs and BOLD responses [16]. DCM is based on a bilinear model of neural population dynamics that is combined with a hemodynamic forward model describing the transformation of



Fig. 3. Intensity of the perceived animacy. The impression of animacy was evaluated with a seven-point scale outside the MRI scanner. The error bars indicate the SEM.

neural activity into a measured BOLD response. In DCM, three sets of parameters are estimated: the direct input to a region (that is, the direct influence of stimuli on regional activity); the baseline connectivity between regions (that is, the interregional influences in the absence of modulating experimental context); and the modulation of connectivity between regions (that is, the changes in the connectivity between regions in the connectivity between regions (that is, the changes in the connectivity between regions induced by the experimental context).

We initially defined the region of interest (ROI) in each subject. To evaluate the effective connectivity in the same hemisphere, we focused on the left OP and the ITG, which showed a main effect of chase [(CO + CN) – (NO + NN)] according to the group analysis with the random effect model. Subject-specific time series were extracted from voxels within a 3-mm radius centered on the local maximum. The time series was high-pass filtered and whitened, and also adjusted by the effects of interest (CO, CN, NO, and NN). We calculated the first principal component of the adjusted time series across all voxels within the ROI and entered this into the DCM.

To constitute the input for the DCM, the model used in the individual analysis was rearranged on factor: visual tracking, and chase and/or obstacle effect, where the NN condition only contained the factor of visual tracking, and CO, NO and CN contained the visual tracking effect and the additional chase, obstacle, and chase and obstacle effects, respectively.

Our anatomical model comprised simple bi-directional baseline connectivity between the OP and the ITG on the left, with the driving input of visual tracking into the OP. The regions were reciprocally connected with baseline connectivity, which was modulated by the chase and/or obstacle effect. All parameters in the DCM were estimated using Bayesian estimation schema for each subject independently.

We defined the effective coupling strength between two regions as the sum of the baseline connectivity and the modulatory effect. Due to our block-design paradigm, the effective coupling strength was systematically changed depending on the condition. For example, the effective coupling strength for the NN condition was equal to the baseline connectivity because there was no chaser or proximity effect. For the CN condition, this was the sum of the baseline connectivity and the modulation by the chase effect. To evaluate the condition-dependent change in the effective coupling strength and its directional dependence, we conducted three-way ($2 \times 2 \times 2$) rmANOVA with direction (OP to ITG vs. ITG to OP), chase, and obstacle effect, using the individual forward and backward effective coupling strength for each condition. This procedure allowed us to summarize the parameters from the subject-specific DCMs and to perform a group analysis for inferences at the group level. A statistical threshold of p < .05 was used to assess the significance of the ANOVAs.

3. Results

3.1. Behavioral data analysis

The performance in the target color-change detection task (Table 1) did not show any significant differences across the condi-

Table 1

Performance in the color-change detection task.

Condition	Reaction tin	ne (ms)	Accuracy (%)
	Mean	SD	Mean	SD
СО	534.0	110.9	90.0	14.4
CN	530.6	99.1	89.0	19.0
NO	517.7	84.5	87.0	21.2
NN	526.5	115.2	88.7	20.3
FIX	503.2	126.6	89.2	19.4

Table 2

Regions commonly activated across four conditions (CO, CN, NO, and NN).

Cluster size (voxels)	Region	BA	Side	MNI coordi	nates		Ζ
				x	у	Z	
26,947	ITS	37	R	50	-66	2	13.69
	ITS	37	L	-44	-68	4	11.83
	SPL	7	R	20	-62	62	10.08
	SPL	7	L	-24	-56	62	11.58
	IOG	18	R	20	-98	-2	9.27
	IOG	18	L	-26	-98	6	8.65
	STS	21/22	R	54	-46	12	3.92
	ITG	37	R	46	-72	-12	4.74
	ITG	37	L	-46	-72	-12	4.53
1,539	FEF	6	R	26	2	50	7.85
2,227	FEF	6	L	-22	-2	52	8.59
398	PO		L	-48	-36	22	5.49
206	Pulvinar		R	20	-28	-2	5.08
258	Pulvinar		L	-22	-28	-4	4.87
63	Cerebellum		L	-26	-36	-50	4.67
96	Cerebellum		R	38	-40	-44	4.05
20	PoCG	1/2	L	-48	-20	32	2.73

BA, Brodmann area; L, left; R, right; FEF, frontal eye field; IOG, inferior occipital gyrus; ITG, inferior temporal gyrus; ITS, inferior temporal sulcus; PO, parietal operculum; PoCG, postcentral gyrus; SPL, superior parietal lobule; STS, superior temporal sulcus. *p* < 0.05 FDR corrected, clusters > 19 voxels are reported.

tions in either reaction time (chase effect, F(1, 27) = 1.5, p = 0.21; obstacle effect, F(1, 27) = 0.04, p = 0.83; chase × obstacle interaction, F(1, 27) = 0.59, p = 0.45, two-way rmANOVA) or accuracy (chase effect, F(1, 27) = 1.98, p = 0.17; obstacle effect, F(1, 27) = 0.037, p = 0.85; interaction, F(1, 27) = 0.77, p = 0.39, two-way rmANOVA). Regarding the animacy score, both of the main effects were statistically significant (chase, F(1, 27) = 135.70, p < 0.001; obstacle, F(1, 27) = 8.54, p < 0.01, two-way rmANOVA) but their interaction was not (F(1, 27) = 4.10, p = 0.053, two-way rmANOVA). Fig. 3 indicates that the chasers more strongly induced the percept of animacy than the obstacles.

3.2. fMRI

The commonly activated areas across all conditions (CO, CN, NO, and NN) compared with the control were the bilateral IOG, the ITG/inferior temporal sulcus (ITS), the superior parietal lobule (SPL), the middle frontal gyrus corresponding to the frontal eye field (FEF) [27], the pulvinar, the cerebellum, the right STS (rSTS) in the right TPJ, the left parietal operculum (PO), and the postcentral gyrus (PoCG) (Fig. 4 and Table 2). The right TPJ, which is a part of the ToM network [20], showed activation with neither a chase effect



Fig. 4. SPM of the common activation across the four conditions (CO, CN, NO, and NN; top), and the activation by the obstacle effect (middle) and by the chase effect (bottom). The results were surface rendered on the transaxial T1-weighted high-resolution MRI. The statistical significance was set at p < 0.05 with an FDR correction for multiple comparisons at the voxel level [22]. The SPM of the obstacle effect and the chase effect was further corrected for multiple comparisons at the cluster level (p < 0.05, cluster size > 100 voxels).

nor an obstacle effect (chase effect, F(1, 27) = 0.25, p = 0.62; obstacle effect, F(1, 27) = 1.12, p = 0.30; chase × obstacle interaction, F(1, 27) = 0.10, p = 0.76) (Fig. 5). This was consistent with our hypothesis that the animacy percept is processed without the involvement of the mentalizing network.

The main effect of obstacle [(CO - CN)+(NO - NN)] revealed a similar activation pattern to the common activation (Fig. 4). By contrast, the main effect of chase [(CO+CN)-(NO+NN)]revealed discrete activations in the bilateral OP and the left ITG (Table 3, Figs. 4 and 6). No area across the whole brain showed a significant interaction. As shown in Fig. 4, the areas with a chase effect markedly overlapped those with an obstacle effect. This warranted the evaluation of the contribution of the chase effect and the obstacle effect to the activation in the overlapped areas. Across these three activated foci, three-way rmANOVA (location × chase × obstacle) showed that the main effects were statically significant (location effect, F(2, 54) = 8.8, p < 0.005; obstacle effect, F(1, 27) = 48.8, p < 0.001), and the interaction across the location and obstacle context was statically significant (F(2, 54) = 11.4, p < 0.001).

To evaluate the contribution of the proximity effect and the animacy effect to the activation more directly, we conducted an rmANCOVA incorporating the contribution of the proximity effect calculated on the basis of the stimuli (Fig. 2), the animacy effect calculated on a perceptual judgment (Fig. 3), the location effect, and their interaction. The animacy scores and proximity scores that were normalized to a zero mean and scaled to a unit range (max to min) were incorporated into the general linear model. The location effect was incorporated as a factor in the repeated measures analysis. There was a significant location × proximity effect interaction (F(2, 108) = 14.68, p < 0.001). By contrast the location × animacy effect interaction was not significant (F(2, 108) = 0.813, p = 0.446). The partial coefficient of the animacy effect

Table 3

Main effect of chase (CO + CN > NO + NN).

Cluster size (voxels)	Region	BA	Side	MNI c	oordinate	s	Ζ
				x	у	Z	
121	ITG	37	L	-46	-72	-8	5.22
802	OP	18	L	-26	-94	-6	5.16
242	OP	18	R	24	-96	-4	4.76

BA, Brodmann area; L, left: R, right; ITG, inferior temporal gyrus; OP, occipital pole. p < 0.05 FDR corrected.



Fig. 5. Activation in the STS. (A) SPM of the common activation across the four conditions (CO, CN, NO, and NN). The result of the conjunction analysis was superimposed on the parasagittal T1-weighted high-resolution MRI data. p < 0.05 with an FDR correction for multiple comparisons. Blue lines cross at (54, -46, 12), corresponding to the rSTS. (B) The effect size of each condition at the STS (cross-hair point). The error bars indicate the SEM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



Fig. 6. Condition-specific activation patterns. SPM of the main effect of the chaser, depicted by the contrast (CN+CO)–(NO+NN) superimposed on a surface-rendered high-resolution MRI unrelated to the subjects of the presented study (center). The bar graphs show the effect size of each condition in the three activated foci: left inferior temporal gyrus (–46, –72, –8), right OP (24, –96, –4), and left OP (–26, –94, –6). The error bars indicate the SEM.

(beta in Table 4) was significant in the left ITG, whereas the proximity effect was significant in the bilateral OP (Table 4). The animacy effect was therefore dominant relative to the proximity effect in the ITG, with the opposite pattern of effects in the OP.

The effective connectivity between ITG and OP was evaluated by the DCM (Fig. 7). The main effects of direction (F(1, 27) = 16.494, p < 0.001), chase (F(1, 27) = 16.556, p < 0.001), and obstacle (F(1, 27) = 57.254, p < 0.001) were all significant. The chase × obstacle interaction was not significant (F(1, 27) = 0.223, p < 0.641). The direction × obstacle interaction was significant (F(1, 27) = 26.108, p < 0.001), whereas the direction × chase interaction was not (F(1, 27) = 1.748, p = 0.197). The direction × chase × obstacle interaction was significant (F(1, 27) = 7.09, p = 0.013). This indicated that the chase effect on the effective connectivity between OP and ITG was bi-directional, whereas the obstacle effect was more prominent in the effective connectivity from ITG to OP than vice versa.

According to their local maximum location in the MNI coordinates, the bilateral OP ((24, -96, -4) and (-26, -94, -6)) corresponded to the kinetic occipital (KO) area [14], and the ITG (-46, -72, -8) corresponded to the lateral occipital complex (LOC) [24,34] (Table 5).

Table 4

Animacy and proximity effects in the ITG and the OP.

Side	Region	MNI coordin	nates		Partial regre	ssion coefficient		
		x	у	Z	Animacy effe	ect	Proximity effe	ect
					Beta	(p)	Beta	(p)
L	ITG	-46	-72	-8	0.638	(0.001)	0.297	(0.196)
L	OP	-26	-94	-6	0.332	(0.152)	1.665	(<0.001)
R	OP	24	-96	-4	0.414	(0.097)	1.238	(<0.001)

Beta is the partial regression coefficient of the normalized animacy scores and the proximity scores of each condition, centered to zero and scaled to unit.



Fig. 7. Effective connectivity from the left OP to the left ITG (red) and vice versa (blue). The error bars indicate the SEM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Typical individual data with a time course plot of the activity are shown in Fig. 8.

4. Discussion

The performance of the visual tracking task did not differ between the conditions. This indicated that across the conditions, equivalent neural activations were produced by the target tracking and color-detection tasks. Thus, we are able to evaluate the neural substrates that were related to the passive percept of animacy.

The present study showed that geometrical objects lacking any morphological cues to identify them as living things appeared to be more animated when their movements were goal-directed, and that the left ITG and the OP played a role in this mode of animacy perception. We found that the bilateral OP showed a more prominent proximity effect than animacy effect, whilst the opposite pattern of effects was observed in the left ITG (Table 3).

Based on previous human fMRI studies, the activated area in the left ITG probably corresponded to the LOC (Table 5), although we did not functionally define these regions. Table 5 shows the close relationships among the KO region, LOC, EBA, and FFA. Regarding the OP, the coordinates did fit with the KO region. However, according to the cytoarchitectonic anatomy data implemented in the Anatomy Toolbox for SPM [15], the most likely fits were Brodmann area (BA) 17 for the coordinates [24, -96, -4] (80% probability; that is, area V1), and BA 18 (30% probability; that is, area V2) and BA 17 (20% probability) for the coordinates [-26, -94, -6]. The KO area might be involved in motion perception, as it has been shown to respond to both kinetic and luminance gratings [14,41]. The KO area is known to process both shape and motion information [14], and responds to the morphological patterns defined by motion [25]. In either case, it is conceivable that the early visual cortex at the OP is involved in the analysis of visual displays evoking the percept of animacy, with



Fig. 8. Individual activation patterns. Individual analysis of the chase effect (green) and the obstacle effect (blue) in the left ITG (upper left, p < 0.005 uncorrected), superimposed on the spatially normalized T1-weighted high-resolution MRI data of this subject in sagittal and coronal sections that cross at (-46, -72, -8). The percentage signal changes during each condition at each location were plotted against the peri-stimulus time (upper right): CO, red; CN, green; NO, blue; and NN, purple. The duration of the condition (0-15 s) is indicated by the yellow-filled column. The data represent the mean values of the nine trials in each subject. The error bars indicate the SEM. The activation pattern and the time course at the left OP (-26, -94, -6; middle row) and the right OP (24, -96, -4; bottom row) are shown in the same format. The chase effect was prominent in the ITG, whereas the obstacle effect was prominent in the OP. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Regions	Talairach (coordinates					MNI coort	dinates					References	Scan types	Subjects nu	nber
	Left			Right			Left			Right						
	×	У	z	×	У	Z	×	у	N	×	У	z				
MT/V5	-47 (4)	-76 (5)	2 (3)	44(3)	-67 (3)	0(5)	-47	-78	-2	44	-69	-4	[13]	fMRI	7	
KO	-8	-94	-4-	34	-88	0	-28	-97	-10	34	91	-2	[14]	PET	10	
L01	-31(4)	-90(5)	1.4(7)	32 (4)	-89(5)	2.6(7)	-31	-92	-4	32	-92	2	[33]	fMRI	15	
L02	-38 (3)	-83 (6)	0 (7)	38 (4)	-82 (5)	1(7)	-38	-85	<u>-</u>	38	-84	-4	[33]	fMRI	15	
LOC	-42 (3)	-73 (8)	-18(10)	42 (3)	-73 (8)	-18(10)	-43	-74	-26	43	-74	-26	[34]	fMRI	9	
Dorsal posterior vertex	-41(5)	-77 (6)	3 (7)	40 (6)	-72 (7)	2(2)	-41	-79	ī	40	-74	-2	[24]	fMRI	4	
Ventral posterior vertex	-36(7)	-71 (7)	-13(5)	37 (5)	-69(7)	-10(4)	-36	-72	-20	37	-71	-16				
Ventral anterior vertex	-38 (5)	-50(6)	-17(5)	33 (4)	-47(6)	-14(4)	-38	-51	-23	33	-48	- 19				
FFA	-35 (3)	-63 (13)	-8(7)	40 (5)	-55(9)	-10(4)	-35	-64	- 14	41	-56	-15	[31]	fMRI	10	
EBA	-50	-69	11	50	-69	4	-51 (4)	-72(5)	8 (4)	51(2)	-71 (4)	1 (3)	[12]*	fMRI	7	
Original data are presents value indicates the mean	:d in Talairact coordinates o	f subjects and	except for [12 d the standard	*, which us deviation is	ed MNI coor s shown in bi	dinates. The c rackets.	onversion be	tween Talair.	ach and MI	VI coordina	ites was perf	ormed wit	h the formula re	ported by Brett	et al. (2001) [6]	Each
about beliefs, inte that the activity in talizing, but might complex biologica associated with co STS, located at the [20], anterior and motion in general	that the region is percept. Previous strated that the rig	are known to be unsurprising as th mentalizing proce	OP, and which is d In the present prefrontal cortex	the model propose process of joint at talizing, is compose this model the per-	between objects e These findings percept are indep	ulation of early vi ventral object pro- LOC and the OP p ties through the i	was more promin the fact that the II be related to obje the idea that the	and only at, the Ol tive connectivity I the chase effect, in regions for the ani	the baseline conr (that is, OP to LO due to the fact tha	of Hasson et al. [2 involvement of th The DCM analy	of the motion relig get and the object the findings of La	LO2, Larsson and H shape information	on two retinotopi eral occipital cort V5/hMT+. LO1 an object-selective L	sion) [34]. Thus, object identificati is motion sensitiv LOC were activate stationary grating	The LOC is re [24,25,34]. The LO by luminance or object recognition	the activity in the

the activity in the LOC being more directly related to the perceived animacy.

The LOC is reported to have a role in object representation [24,25,34]. The LOC responds to the morphological patterns defined by luminance or motion [25] and activation is enhanced when object recognition is increased through blurring (the Lincoln illusion) [34]. Thus, the LOC activity is specifically correlated with object identification by morphological cues. Furthermore, the LOC is motion sensitive: dorsal occipito-temporal regions including the LOC were activated by a low-contrast moving ring compared with stationary gratings [28]. Recently, Larsson and Heeger [33] reported on two retinotopic visual areas, LO1 and LO2, in the human lateral occipital cortex between the dorsal part of visual area V3 and V5/hMT+. LO1 and LO2 overlapped with the posterior part of the object-selective LOC and KO area. Based on the combination of complex shape selectivity and retinotopic organization of LO1 and LO2, Larsson and Heeger [33] suggested that LO1 and LO2 integrate shape information from multiple visual submodalities in retinotopic coordinates [33]. In the present study, the goal-directedness of the motion relied on the dynamic relationship between the target and the object represented in retinotopic coordinates. Thus, the findings of Larsson and Heeger [33] in conjunction with that of Hasson et al. [28] are consistent with the present results of the involvement of the LOC and OP in the animacy percept.

The DCM analysis between the left ITG and the OP showed that the baseline connectivity (NN) had a significant direction effect (that is, OP to LOC rather than vice versa). This might have been due to the fact that the driving input of visual tracking entered at, and only at, the OP, and was thus an asymmetrical input. The effective connectivity between them was bi-directionally enhanced by the chase effect, indicating the functional integration of these two regions for the animacy percept, whereas the OP to ITG modulation was more prominent than vice versa for the obstacles. Considering the fact that the ITG might correspond to the LOC, and hence might be related to object representation, this finding is consistent with the idea that the animacy percept arises from the top-down modulation of early visual areas (the OP) by more anterior sites in the ventral object processing pathways (the LOC). We conclude that the LOC and the OP play a role in the identification of animated entities, through the integration of information about the relationship between objects encoded in retinotopic coordinates.

These findings suggest that the neural substrates of the animacy percept are independent of mentalizing, which is consistent with the model proposed by Baron-Cohen [2]. He suggested that the process of joint attention, which is an important example of mentalizing, is composed of the ID, EDD, SAM, and ToMM. According to this model, the percept of animacy corresponds to the ID, which we propose is represented in the interaction between the LOC and the OP, and which is distinct from the ToMM.

In the present study, no activation was found in the medial prefrontal cortex or the temporal poles, which are regions that are known to be involved in mentalizing tasks. This might be unsurprising as the present task minimized the need for top-down mentalizing processes. However, the right TPJ was activated in conditions that lacked a chase or obstacle effect (Fig. 5), indicating that the region is not associated with the degree of the animacy percept. Previous neuroimaging studies have consistently demonstrated that the right TPJ is activated in tasks that require reasoning about beliefs, intentions, or thoughts [11]. It has been suggested that the activity in the right TPJ might not be selective for mentalizing, but might be more broadly involved in the perception of complex biological motion [35]. The right TPJ activation might be associated with complex visual motion processing in the posterior STS, located at the TPJ and extending towards the angular gyrus [20], anterior and superior to the MT/V5, which respond to visual motion in general [13,46,47]. The posterior STS is well known to be activated by the observation of biological motion [1,43], such as moving bodies and body parts [7,42], and even by action that is reduced to moving points of light [5,23,26]. Maquet et al. [35] showed that learning to follow complex but predictable patterns of movement activated this region. They concluded that the STS was not specifically concerned with the behavior of living things or social cues, but more generally with the evaluation of complex motion patterns [35]. Frith and Frith [20] pointed out that complex patterns of movement were more likely to be associated with living things than with physical systems. In the present study, the trajectories of the target object were identical across the conditions, and the subjects tracked the complex but slow trajectories without any explicit mentalizing task. This resulted in the constant activation of the right TPJ.

A previous study by Schultz et al. [44] showed that the amount of interaction between two moving objects modulated the percept of animacy, and positively correlated with the activity of the posterior STS/STG. We speculate that this discrepancy in findings might be due to differences in the stimulus characteristics. Schultz et al. [44] adopted relatively high object speeds, ranging from 6 to $20^{\circ}/s$, correlated with the level of cross-correlation in object movement. They compared an interactive condition with a control condition in which the object movement was unrelated but the object speed was conserved. Both animacy and speed ratings were collected. Effects of task were not found in the posterior STS/STG. They suggested that the amount of mentalizing involved did not differ between the tasks. At the lower level of motion cross-correlation, with slower speed, the perception of animacy showed little change, but no activation was observed in the posterior STS/STG (Fig. 5 in [44]). It is possible that an increase in the interactivity and speed of an object might induce reorientations in attention, represented by activity in the right TPJ [10,37]. Thus, the response of the STS by means of the interaction/animacy might depend on the speed of the object's movement.

The activation of the STS by the recognition of biological motion is known to be influenced by concurrent mentalizing tasks performed by the subjects [4]. Using complex, abstract moving objects in a chasing scenario, Schultz et al. [45] found that the posterior STS/STG was more prominently activated when the subjects had to identify the strategy rather than the outcome of the chase [45]. The authors speculated that this was caused by a simplified form of mental status attribution [20]. Considering the fact that the right TPJ, including the posterior STS, is related to mentalizing and biological motion processing, the right TPJ might be the node that connects the ID and ToMM, and forms a link that can be modulated by the top-down effect of task requirement (that is, mentalizing).

In this experiment, the psychophysical evaluation of animacy was performed without a visual tracking task. By contrast, the subject underwent the visual tracking task without the overt evaluation of the animacy percept during fMRI. This raises the possibility that the perceived animacy might have differed between the pre-scan session and during the fMRI. To clarify this point, we recruited a further 15 healthy subjects (4 females; 11 males; mean age = 24.3 ± 3.3 years; all right handed). The subjects were required to conduct the target color-change detection task in the same manner as in the fMRI experiment, visually tracking the target throughout, and evaluating the degree of animacy of the target red disk, after the completion of each task session in 15 s, on a sevenpoint scale. The animacy scores for each condition were as follows: CO = 4.73 (SD = 1.20); CN = 4.42 (SD = 1.05); NO = 3.70 (SD = 1.03); and NN = 3.38 (SD = 1.05). Two-way rmANOVA of the animacy score revealed that both of the main effects were statistically significant (chase, F(1, 14) = 22.33, p < 0.001; obstacle, F(1, 14) = 7.08, p < 0.05), but their interaction was not (F(1, 14) = 0.005, p = 0.95). This indicated that the chase effect was more prominent than the obstacle effect in the percept of animacy, even during the visual tracking task. This result confirmed that the animacy percept was mainly determined by the presence of a chaser, regardless of any concomitant visual tracking task. Notably, one limitation of the study was that direct measurement of the eye movement during fMRI was not performed due to technical challenges. Despite this, the high performance in the target color-change detection task indicated that the subjects were successfully tracking the moving cue.

5. Conclusion

The present study showed that the animacy percept, which is related to the identification of animated objects via visual motion cues, is associated with early visual processing in regions of the ventral visual pathways, such as the OP and the LOC, in the absence of any explicit mentalizing task. These areas might represent neural correlates for ID [2] in models of joint attention.

Conflict of interest

All authors declare that there is no conflict of interest.

Acknowledgments

The authors appreciate Dr. D.N. Saito for the discussion regarding the task design. This study was supported in part by Grant-in Aid for Scientific Research S#17100003 (to NS) from the Japan Society for the Promotion of Science.

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