

The “vegetarian brain”: chatting with monkeys and pigs?

Massimo Filippi · Gianna Riccitelli ·
Alessandro Meani · Andrea Falini ·
Giancarlo Comi · Maria A. Rocca

Received: 26 April 2012 / Accepted: 8 September 2012 / Published online: 29 September 2012
© Springer-Verlag 2012

Abstract An array of brain regions in the fronto-parietal and temporal lobes cooperates to process observation and execution of actions performed by other individuals. Using functional MRI, we hypothesized that vegetarians and vegans might show brain responses to mouth actions performed by humans, monkeys, and pigs different from omnivores. We scanned 20 omnivores, 19 vegetarians, and 21 vegans while watching a series of silent videos, which presented a single mouth action performed by a human, a monkey, and a pig. Compared to omnivores, vegetarians and vegans have increased functional connectivity between regions of the fronto-parietal and temporal lobes versus the cerebellum during observation of mouth actions performed by humans and, to the same degree, animals. Vegans also had increased connectivity with the supplementary motor area. During human mouth actions, increased amygdala activity in vegetarians and vegans was found. More critically, vegetarians recruited the right middle frontal gyrus and insula, which are involved in social mirroring, whereas vegans activated the left inferior frontal gyrus and middle temporal gyrus, which are part of the mirror neuron system. Monkey mouth actions triggered language network activity

in both groups, which might be due to the attempt to decode monkey mouth gesture, with an additional recruitment of associative temporo-occipital areas in vegans, whereas pig mouth actions activated empathy-related regions, including the anterior cingulum. These results support the role of the action observation–execution matching system in social cognition, which enables us to interact not only with our conspecifics but also with species in phylogenetic proximity to humans.

Keywords Action observation–execution matching system · Animals · Humans · Mouth action · Vegetarians

Introduction

Processing and understanding actions performed with the mouth by other individuals contribute to infer other people’s emotional states and intentions, which is a hallmark of social interaction. Functional imaging investigations have identified a set of brain areas, located mainly in the parietal and frontal lobes, which are activated consistently, together with several extrastriate occipital areas, during the observation of mouth actions performed not only by humans but also by other species (i.e., monkeys and dogs) (Buccino et al. 2004). Remarkably, while actions belonging to the observer’s repertoire (e.g., speech reading) are mapped in areas of the motor system located in the inferior frontal gyrus (IFG), which include Broca’s area (BA44/BA45), actions which are not part of such a repertoire (e.g., barking) are processed on the basis of their visual properties and mapped to visual areas (Buccino et al. 2004). Converging pieces of evidence suggest that the neuronal network that involves the IFG and the inferior parietal lobule (IPL), which form part of the mirror neuron system (MNS), is also necessary for emotion

M. Filippi (✉) · G. Riccitelli · A. Meani · M. A. Rocca
Neuroimaging Research Unit, Institute of Experimental
Neurology, Division of Neuroscience, San Raffaele Scientific
Institute, “Vita-Salute” San Raffaele University,
Via Olgettina 60, 20132 Milan, Italy
e-mail: filippi.massimo@hsr.it

M. Filippi · G. Comi · M. A. Rocca
Department of Neurology, San Raffaele Scientific Institute,
“Vita-Salute” San Raffaele University, Milan, Italy

A. Falini
Department of Neuroradiology, San Raffaele Scientific Institute,
“Vita-Salute” San Raffaele University, Milan, Italy

recognition and contagion, which contribute to emotional empathy (Shamay-Tsoory 2011; Shamay-Tsoory et al. 2009). Several factors modulate empathic response, including the subjective attitude held toward the observed individual (Singer et al. 2006) and personal experience (Cheng et al. 2007). A recent fMRI investigation has demonstrated that the neuronal representation of empathy differs among individuals with different dietary habits due to ethical reasons (i.e., vegetarians and vegans vs. omnivores) (Filippi et al. 2010). Specifically, when compared to omnivores, both vegetarians and vegans recruit different areas of the empathy network during observation of negative affective pictures (showing mutilations, murdered people, human/animal threat, torture, etc.) of human beings and, more critically, animals. Substantial differences between vegetarians and vegans were also found, with a prevailing activity of the anterior cingulum in vegetarians and of the IFG in vegans, possibly reflecting different motivational factors and beliefs.

With this background in mind, we hypothesized that the representation of mouth actions within different brain regions might differ among individuals with different dietary habits and ethical beliefs during processing of actions performed by other humans and other species. We assumed that, due to their propensity to identify nonconspicuous as being like themselves, and their increased empathic response towards animal actions, when compared to omnivores, vegetarians and vegans would exhibit a different pattern of recruitment of regions involved in the processing of mouth actions, including those located in the fronto-parietal lobes. We also supposed that, since different motivational factors and beliefs characterize vegetarianism and veganism, with the first being linked to the notion of not performing direct violence towards animals and the second being against the rights of humans to use animals in any way (Regan 1985), in addition to a common-shared pattern of cortical processing of mouth actions, vegetarians and vegans might also experience functional architecture differences. Finally, we postulated that the recruitment of the previous regions might differ according to the species involved and their phylogenetic proximity to humans.

Experimental procedure

The study was approved by the Ethics Committee of Scientific Institute and University Hospital San Raffaele, Milan, Italy and written informed consent was obtained from all subjects prior to study entry.

Subjects

We studied 60 right-handed (Oldfield 1971) human healthy subjects (34 women and 26 men; mean age 37.7, range

18–60 years) with different dietary habits. All subjects had normal or corrected-to-normal vision. We recruited 20 omnivores (11 women and 9 men; mean age 36.9, range 22–60 years), 19 vegetarians (11 women and 8 men; mean age 40.3, range 23–60 years), and 21 vegans (12 women and 9 men; mean age 36.3, range 18–53 years). The groups did not differ statistically in sex, age, or level of education. A questionnaire was completed by all subjects before fMRI acquisition to investigate eating habits, reasons and motivations for eating choices, and the time elapsed from making this choice. All vegetarians and vegans reported that they made their dietary choice for ethical reasons. They had had stable eating habits for a mean of 3.8 years (SD 8.7 years), and were recruited from vegetarian societies. Omnivore subjects were recruited by advertisement, and none of them had been vegetarian or vegan before the study. Eight vegans had been vegetarian before becoming vegan. All the subjects were naïve about the nature of the study. None of the subjects had any history of neurological, major medical, or psychiatric disorders, or either alcohol or drug abuse. None of the subjects was taking any medical treatment at the time of fMRI assessment.

Experimental design

Using a block design, all subjects were scanned while watching a series of silent videos, which presented a single mouth action performed by a human, a monkey, and a pig in each block (Fig. 1). According to the experiment of Buccino (Buccino et al. 2004), the mouth actions observed were (1) biting, and (2) oral communicative actions (OCAs). However, our experiment differed from that of Buccino, since we investigated pig rather than dog actions, because we thought that dogs were likely to raise a similar degree of sympathy in the different study groups. Furthermore, monkey scenes were recorded in a free environment. The videos were delivered using the Presentation software. Participants were instructed to look at the scenes focusing their attention on mouth movements, without providing any specific response during the fMRI acquisition. Each block consisted of 12 s of video, followed by a 12 s resting period. During each block, the same action (i.e., biting or OCAs) was presented four times. During the resting phase of a given block, the subjects had to observe a static frame of the same action for 12 s. Each of the six blocks of the experiment was performed four times within a run. The order of videos in the various blocks was counter-balanced across subjects. Two runs were performed for each subject and averaged during the fMRI statistical analysis.

fMRI acquisition

Using a 3.0 T scanner (Intera, Philips Medical Systems, Best, The Netherlands) fMRI scans were acquired using a

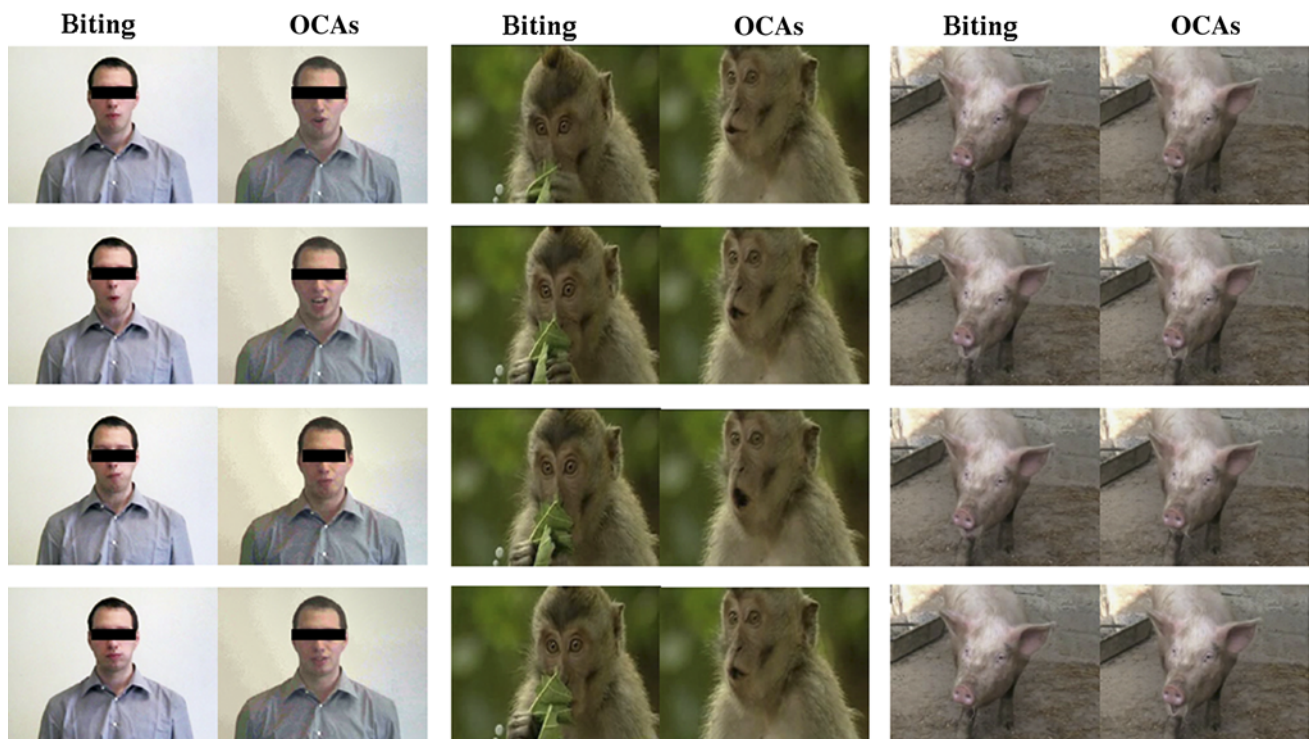


Fig. 1 Selected frames from the videos showing biting and oral communicative actions (OCAs) performed by a human, a monkey, and a pig

T2*-weighted single-shot echo-planar imaging (EPI) pulse sequence [echo time (TE) = 30 ms, flip angle = 85°, matrix size = 128 × 128, field of view (FOV) = 240 mm × 240 mm, repetition time (TR) = 3.0 s]. During each functional scanning run, 192 sets of 40 axial slices, parallel to the anterior–posterior commissural plane, with a thickness of 3 mm, were acquired. Head movements were minimized using foam padding.

In the same scanning session, a brain dual-echo turbo spin echo sequence (TR = 3,500 ms, TE = 24/120 ms; echo train length = 5; flip angle = 150°, 44 contiguous, 3-mm-thick, axial slices with a matrix size = 256 × 256 and a FOV = 240 mm × 240 mm) was also acquired to check for MRI lesions/abnormalities.

All subjects reported that they had not fallen asleep during scanning, according to a questionnaire delivered immediately after the MRI session.

fMRI analysis

fMRI data were analyzed using the statistical parametric mapping (SPM8) software. Prior to statistical analysis, all images were realigned to the first one of the series to correct for subject motion, spatially normalized into the Montreal Neurological Institute (MNI) space, and smoothed with a 3-D 10 mm FWHM Gaussian filter.

Statistical analysis

Analysis of activations

Changes in blood oxygen level-dependent contrast associated with each condition were assessed using the general linear model (Friston et al. 1995). In each subject, a first-level design matrix was built, where subject motion parameters were used as regressors of no interest. Then, specific effects were tested by applying appropriate linear contrasts. For each subject, activation maps were first derived by contrasting each active condition with its own control condition, with the following contrasts defined: human biting > static human biting; monkey biting > static monkey biting; pig biting > static pig biting; human OCAs > static human OCAs; monkey OCAs > static monkey OCAs; pig OCAs > static pig OCAs. Significant hemodynamic changes for each contrast were assessed using *t* statistical parametric maps (SPM_t). Second level random effect analyses, using 3 × 2 ANOVA models, in which stimuli (3) and conditions (2) were entered as separate factors, were performed to assess the main effects of the stimuli (i.e., human, monkey, and pig) and conditions (i.e., biting and OCA) within the three groups of subjects of the study (i.e., omnivores, vegetarians, and vegans). Between-group differences were assessed by means of 3 × 3 or 3 × 2 ANOVA models, when comparing among

the three groups the effect of stimuli or conditions, respectively (Friston et al. 1999). The following sets of linear comparisons were performed: (1) vegetarians and vegans, separately, versus omnivores; (2) vegetarians and vegans, combined, versus omnivores; (3) vegetarians versus vegans, and vice versa. Common patterns of activation between vegetarians and vegans during a given contrast as well as regions of specific activations of each group contrasted to the others were identified by a conjunction analysis (Friston et al. 2005).

We report activations below a threshold of $p < 0.05$ corrected for multiple comparisons [family-wise error (FWE)]. The identification of regions of activation was performed using the Anatomical Automatic Labeling (aal) atlas (Tzourio-Mazoyer et al. 2002) and the Brodmann area (BA) atlas (Lancaster et al. 2000; Maldjian et al. 2003).

To compare the location of activations within the different portions of the IFG involved in mouth actions (i.e., pars opercularis and pars triangularis) between groups and during the different experimental conditions, the MNI coordinates of all peaks showing significant activations in each single subject's analysis were extracted using the WFU Pickatlas software package and masks of BA44 (corresponding to pars opercularis) and BA45 (corresponding to pars triangularis) (Lancaster et al. 2000; Maldjian et al. 2003), and then compared between groups using the SPSS software and ANOVA models ($p < 0.05$). This analysis was driven by the consideration that these two portions of the L IFG are known to be involved in different functions: the pars opercularis being supposed to contain MN involved in processing mouth actions (Buccino et al. 2001; Tettamanti et al. 2005), whereas the pars triangularis has been consistently found to be activated across semantic studies employing different design paradigms (Xiang et al. 2010).

Analysis of functional connectivity (FC)

The realigned and normalized fMRI data entered a FC analysis using a seed-voxel correlation approach (Biswal et al. 1995). FC analysis estimates how strong the associations are between observed time series, without investigating the causal relationships between them. For this analysis, fMRI time series were first pre-processed to reduce data variability unlikely to reflect neuronal activity. These additional pre-processing steps comprised temporal band-pass filtering ($0.009 \text{ Hz} < f < 0.08 \text{ Hz}$) and spatial smoothing with a 3-D 6 mm FWHM Gaussian filter (Fox et al. 2005). Then, the time series were processed in two steps: first, we selected a ROI to serve as a seed region for correlation; subsequently, we performed a regression analysis between this seed region and all the remaining voxels of the brain. The definition of the seed reference

time course for FC analysis relied on the maps of left BA44/BA45 (Broca's region) and BA21/BA22 available in the WFU Pickatlas (Lancaster et al. 2000; Maldjian et al. 2003). Two anatomical masks for the left BA44/BA45 and the left BA21/BA22 were created using WFU Pickatlas (Maldjian et al. 2003) and, for each subject, the average time series within these ROIs, separately, were extracted. FC was then investigated using SPM8 and multiple regression models, including as covariate of interest the time series extracted from the reference seed region, and as confounding covariates: (1) the six motion parameters obtained during the rigid-body motion correction step, (2) the whole brain signal averaged over the entire tissue, (3) the averaged ventricular signal and, (4) the averaged white matter signal (Fox et al. 2005). This analysis generated a statistical FC map of the left BA44/BA45 region for each subject. Similarly, a statistical FC map of the left BA21/BA22 was produced. Within-group and between-group comparisons of these FC maps were assessed using SPM8 one-sample t tests and ANOVA models, respectively ($p < 0.05$, FWE corrected).

Analysis of demographic and behavioural data

Demographic data were compared using SPSS and an ANOVA model. Post hoc comparisons were corrected for multiple comparisons using Bonferroni correction.

Results

Biting

Tables 1, 2 and 3 summarize the results of between-group comparisons during the different experimental conditions. During “human scenes”, compared to vegetarians and vegans, omnivores had increased activity of the left parahippocampal gyrus, right putamen, left insula, and left inferior occipital gyrus (IOG) (BA19). Compared to omnivores and vegans, vegetarians had increased activity of the left cerebellum (crus I) and right IFG, pars opercularis (BA44). Compared to omnivores and vegetarians, vegans had increased activation of the right superior temporal gyrus (STG) (BA21). Compared to vegetarians, vegans also had increased activity of the left middle temporal gyrus (MTG). During “monkey scenes”, compared to omnivores, vegetarians and vegans had increased activity of the bilateral amygdala. Compared to omnivores, vegetarians had additional increased activity of the right supramarginal gyrus (SMG), right middle occipital gyrus (MOG), and right IFG, pars triangularis (BA45). Finally, compared to omnivores and vegetarians, vegans had additional increased activity of the bilateral MTG (BA21).

Table 1 Areas significantly more activated (activation sites and Montreal Neurological Institute coordinates) in omnivores versus vegetarians and vegans during biting and oral communicative action scenes (ANOVA, $p < 0.05$ family-wise error corrected)

Condition	Activation sites	Omnivores					
		Human scenes		Monkey scenes		Pig scenes	
		Versus vegetarians and vegans	Versus vegetarians only	Versus vegetarians and vegans	Versus vegetarians only	Versus vegetarians and vegans	Versus vegetarians only
Biting	L parahippocampal gyrus	-20, -38, 0	-	-	-	-	-
	R putamen	26, 16, 6	-	-	-	-	-
	L insula	-24, 12, -10	-	-	-	-	-
	L IOG	-42, -68, -4	-	-	-	-	-
OcAs	-	-	-	-	-	-	-

R right, L left, IOG inferior occipital gyrus, OcAs oral communicative actions

During “pig scenes”, compared to omnivores and vegans, vegetarians had increased activity of the right IFG, pars opercularis (BA44). Compared to omnivores, they also had increased activity of the right SMG, whereas compared to vegans they had increased activity of the left fusiform gyrus and left cerebellum (crus II). Compared to omnivores and vegetarians, vegans had increased activity of the left MTG (BA21) and left MOG.

OcAs

No between-group differences were detected during “human scenes”. During “monkey scenes”, compared to omnivores, vegetarians and vegans had increased activity of the bilateral calcarine cortex, and left MTG (BA22, Wernicke’s area). Compared to omnivores and vegans, vegetarians had increased activity of the left IFG, pars triangularis (BA45). Compared to omnivores, vegetarians also had increased activity of another cluster in the left MTG (BA21) and left precentral gyrus. Compared to omnivores and vegetarians, vegans had increased activity of the right MTG (BA21) and right MOG. Compared to omnivores, vegans also had increased activity of the left MOG. During “pig scenes”, compared to omnivores and vegans, vegetarians had increased activity of the anterior cingulum. Compared to omnivores and vegetarians, vegans had increased activity of the left MTG (BA 21), left IFG, pars triangularis (BA45), and bilateral middle frontal gyrus (MFG). Finally, compared to vegetarians, vegans also had increased activity of the right parahippocampal gyrus.

OcAs versus biting

The results of the within-group comparisons of biting versus OcAs and vice versa, in the three study groups, are summarized in Tables 4 and 5 and are shown in Fig. 2. During “human scenes”, vegetarians and vegans versus omnivores had an increased activity of the right amygdala. Compared to the other two groups, vegetarians had a selective increased recruitment of the right MFG and the posterior portion of the right insula (MNI coordinates: 38, -10, 8), whereas vegans recruited selectively the left MFG, left IFG (pars opercularis) and left MTG, posterior part (BA37) (MNI coordinates: -48, -56, -2). During “monkey scenes”, vegetarians and vegans versus omnivores had increased activity of the bilateral cuneus and left MTG (BA22) (MNI coordinates: -62, -44, 8). Vegetarians selectively activated the left MTG (BA21), posterior portion (MNI coordinates: -52, -52, 16) and IFG (pars opercularis), and vegans the right MTG (BA21), anterior portion (MNI coordinates: 56, 2, -16) and MOG. During “pig scenes”, vegetarians showed a selective increased activity of the anterior cingulum and vegans activated the bilateral parahippocampal gyrus (Fig. 3).

Table 2 Areas significantly more activated (activation sites and Montreal Neurological Institute coordinates) in vegetarians versus omnivores and vegans during biting and oral communicative action scenes (ANOVA, $p < 0.05$ family-wise error corrected)

Condition	Activation sites	Vegetarians								
		Human scenes			Monkey scenes			Pig scenes		
		Versus omnivores and vegans	Versus omnivores only	Versus vegans only	Versus omnivores and vegans	Versus omnivores only	Versus vegans only	Versus omnivores and vegans	Versus omnivores only	Versus vegans only
Biting	L cerebellum	-32, -74, -36	-	-	-	-	-	-	-	-26, -80, -46
	R IFG	46, 14, 10	-	-	-	40, 36, 0	-	34, 6, 34	-	-
	R amygdala	-	-	-	-	16, -12, -14	-	-	-	-
	L amygdala	-	-	-	-	-20, -4, -10	-	-	-	-
	R SMG	-	-	-	-	54, -34, 40	-	-	56, -4, -26	-
	R MOG	-	-	-	-	32, -66, 34	-	-	-	-
	L fusiform gyrus	-	-	-	-	-	-	-	-	-28, -24, -26
OCAs	R calcarine cortex	-	-	-	-	4, -78, 14	-	-	-	-
	L calcarine cortex	-	-	-	-	-2, -80, 18	-	-	-	-
	L MTG	-	-	-	-	-58, -18, -2	-	-	-	-
		-	-	-	-	-56, 4, 14	-	-	-	-
	L IFG	-	-	-	38, 26, 14	-	-	-	-	-
	L precentral gyrus	-	-	-	-	-50, 14, 32	-	-	-	-
	Anterior cingulum	-	-	-	-	-	-	6, 42, 10	-	-

OCAs oral communicative actions, R right, L left, IFG inferior frontal gyrus, SMG supramarginal gyrus, MOG middle occipital gyrus, MTG middle temporal gyrus

Species-related recruitment

To assess whether the activity of regions associated with OCA scenes differed in the three groups according to the species observed (i.e., human, monkey, pig), a within-group comparison of species-related activations during OCAs was performed. The results of this analysis are summarized in Table 6. During human versus monkey OCAs, compared to vegetarians and vegans, omnivores had an increased activity of the right IOG and STG (MNI coordinate: -50, -18, -2). Vegans had selective increased activity of the left MTG, posterior part (MNI coordinates: -46, -56, -2), right precentral gyrus and left IFG (MNI coordinates: -48, 2, 14). During human versus pig OCAs, omnivores versus vegetarians and vegans had increased activation of the anterior portion of the right insula (MNI coordinates: 36, 30, 6), and left IFG (pars triangularis) (MNI coordinates: -36, 20, 26).

Vegetarians and vegans versus omnivores had increased recruitment of the anterior lobe of the cerebellum (MNI coordinates: -26, -44, -22). Vegetarians had selective increased activity of the right amygdala, whereas vegans activated the right precentral gyrus. During monkey versus pig OCAs, vegetarians and vegans versus omnivores had increased activity of the right amygdala, bilateral superior parietal lobule (SPL) and right IOG. Vegetarians had selective increased activity of the right globus pallidus (Fig. 4).

Location of IFG activity

A region of interest (ROI) analysis was performed to compare the locations of activation in the different portion of the IFG involved in mouth actions between groups and during the different experimental conditions. In all three study groups, activity within the left BA44 and BA45 was

Table 3 Areas significantly more activated (activation sites and Montreal Neurological Institute coordinates) in vegans versus omnivores and vegetarians during biting and oral communicative action scenes (ANOVA, $p < 0.05$ family-wise error corrected)

Condition	Activation sites	Vegans														
		Human scenes				Monkey scenes				Pig scenes						
		Versus omnivores and vegetarians	Versus omnivores only	Versus vegetarians only	Versus omnivores and vegetarians	Versus omnivores only	Versus vegetarians only	Versus omnivores and vegetarians	Versus omnivores only	Versus vegetarians only	Versus omnivores and vegetarians	Versus omnivores only	Versus vegetarians only			
Biting	R STG	64, -4, -48	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	L MTG	-	-	-48, -70, 16	-52, -56, 14	-	-	-	-	-	-54, -52, 12	-	-	-	-	-
	R MTG	-	-	-	48, -60, 18	-	-	-	-	-	-	-	-	-	-	-
	R amygdala	-	-	-	-	16, -12, -14	-	-	-	-	-	-	-	-	-	-
	L amygdala	-	-	-	-	-20, -4, -10	-	-	-	-	-	-	-	-	-	-
	L MOG	-	-	-	-	-	-46, -70, 16	-	-	-	-	-	-	-	-	-
OCAs	R calcarine cortex	-	-	-	-	4, -78, 14	-	-	-	-	-	-	-	-	-	-
	L calcarine cortex	-	-	-	-	-2, -80, 18	-	-	-	-	-	-	-	-	-	-
	L MTG	-	-	-	-	-58, -18, -2	-	-	-	-	-56, -52, 12	-	-	-	-	-
	R MTG	-	-	-	50, -50, 14	-	-	-	-	-	-	-	-	-	-	-
	L MOG	-	-	-	-	-32, -94, -4	-	-	-	-	-	-	-	-	-	-
	R MOG	-	-	-	36, -92, 6	-	-	-	-	-	-	-	-	-	-	-
	L IFG	-	-	-	-	-	-	-	-	-	-38, 20, 28	-	-	-	-	-
	L MFG	-	-	-	-	-	-	-	-	-	32, 26, 40	-	-	-	-	-
	R MFG	-	-	-	-	-	-	-	-	-	-20, 38, 22	-	-	-	-	-
	R parahippocampal gyrus	-	-	-	-	-	-	-	-	-	-	-	-	-	34, -30, -12	-

OCAs: oral communicative actions, R right, L left, STG superior temporal gyrus, IFG inferior frontal gyrus, MFG middle frontal gyrus, MOG middle occipital gyrus, MTG middle temporal gyrus

Table 4 Within-group comparisons (activation sites and Montreal Neurological Institute coordinates) of biting versus oral communicative action scenes of human, monkey and pig in omnivores, vegetarians and vegans (paired *t* test in each group, *p* < 0.05 family-wise error corrected)

Activation sites	Side	Human scenes			Monkey scenes			Pig scenes		
		Omnivores	Vegetarians	Vegans	Omnivores	Vegetarians	Vegans	Omnivores	Vegetarians	Vegans
MOG	L	-44, -74, 12	-26, -98, 16	-24, -100, 8	-36, -90, 2	-52, -78, 2	-46, -84, -2	-44, -72, 2	-48, -72, 6	-
IOG	L	-	-	-	-48, -74, -6	-44, -82, -4	-36, -90, -8	-40, -80, -2	-36, -76, -8	-
	R	-	-	-	30, -88, -12	-	46, -76, -4	-	36, -76, -4	-
ITG	R	46, -66, -2	48, -54, -12	-	48, -70, -4	46, -66, -6	46, -50, -24	52, -72, -4	-	-
MTG	R	-	-	-	-	48, -62, 2	46, -60, 2	58, -70, 6	42, -66, 6	-
IPL	L	-	-	-	-32, -56, 52	-	-	-	-	-
	R	-	-	-	32, -40, 50	32, -52, 52	-	-	-	-
SPL	R	32, -68, 54	30, -74, 50	-	34, -56, 60	-	38, -46, 60	-	-	-
Hippocampus	R	-	-	-	-	20, -28, -6	-	-	-	-
Cerebellum	L	-	-44, -48, -36	-24, -88, -30	-48, -52, 28	-42, -62, -24	-40, -56, -22	-	-20, -38, -22	-
	R	-	26, -80, -26	48, -52, -26	36, -46, -26	34, -64, -24	44, -66, -20	-	-	-
Cuneus	L	-10, -102, 6	-4, -102, 16	-	-	-	-	-	-	-
	R	14, -98, 24	14, -80, 44	12, -104, 10	12, -86, 42	-	-	24, -100, 12	-	-
Fusiform gyrus	L	-	-34, 54, -18	-	-	-40, -48, -24	-36, -68, -12	-	-	-
	R	38, -44, -24	-	-	40, -56, -16	-	-	-	30, -48, -14	-
Postcentral gyrus	L	-	-	-	-	-	-	-	-	-32, -30, 52

R right, L left, MOG middle occipital gyrus, IOG inferior occipital gyrus, ITG inferior temporal gyrus, MTG middle temporal gyrus, IPL inferior parietal lobule, SPL superior parietal lobule

higher during human than “monkey” and “pig scenes”. Vegetarians had a cranial shift (*z* coordinate = 16) (ANOVA model, *p* = 0.02) of the center of activation of the left BA44 during the pig OCA scenes, compared to omnivores (*z* coordinate = 11, *p* = 0.05 corrected) and vegans (*z* coordinate = 11, *p* = 0.05 corrected), whereas vegans had a posterior shift (ANOVA model, *p* = 0.04) of the center of activation of the right BA45 during human OCAs (*y* coordinate = 21) versus omnivores (*y* coordinate = 27) (Fig. 5).

FC analysis

The results of the analysis of FC within each study group using the BA44/BA45 and the BA21/BA22, respectively, as seed

regions are shown in Fig. 6. The analysis of left BA44/BA45 FC showed that, compared to vegetarians and vegans, omnivores had increased FC between the left BA44/BA45 and the bilateral SMG and right STG. Compared to omnivores, vegetarians and vegans had increased FC with the right cerebellum (crus I). Compared to the other two groups, vegetarians had a selective increased FC with the right BA45 and the bilateral BA48, whereas vegans had a selective increased FC with the right supplementary motor area (SMA). The analysis of left BA21/BA22 FC showed that, compared to vegetarians and vegans, omnivores had increased FC between the left BA21/BA22 and the right MTG and left IFG. Compared to omnivores, vegetarians and vegans had increased FC with the right cerebellum (crus I) and right postcentral gyrus. Compared to the other two groups, vegetarians had a selective increased FC with the right IFG (BA44/BA45) and the left

Table 5 Within-group comparisons (activation sites and Montreal Neurological Institute coordinates) of oral communicative action versus biting scenes of human, monkey and pig in omnivores, vegetarians and vegans (paired *t* test in each group, *p* < 0.05 family-wise error corrected)

Activation sites	Side	Human scenes			Monkey scenes			Pig scenes		
		Omnivores	Vegetarians	Vegans	Omnivores	Vegetarians	Vegans	Omnivores	Vegetarians	Vegans
Postcentral gyrus	L	–	–58, –12, 40	–36, –24, 40	–	–	–22, –32, 62	–	–	–
	R	–	–	–	–	–	–	24, –32, 70	–	–
Precentral gyrus	L	–	–	–28, –10, 52	–	–	–20, –14, 70	–	–	–
Precuneus	L	–	–	–	–32, –52, 14	–16, –50, 22	–10, –44, 46	–	–	–
	R	–	18, –44, 4	–	22, –44, 12	20, –48, 14	14, –40, 44	–	–	–
SFG	L	–	–	–20, 36, 36	–16, 42, 18	–	–28, 44, 38	–	–	–
	R	–	–	–	26, 14, 60	–	–	–	–	–
IFG (BA45)	L	–	–	–36, 38, 2	–	–40, 24, 10	–	–	–	–54, 26, 16
	R	46, 20, 4	–	–	–	–	–	–	–	–
IFG (BA44)	L	–	–	–48, 12, 16	–	–48, 12, 16	–56, 10, 14	–	–	–
	R	–	–	–	–	40, 14, 12	–	–	–	–
STG	L	–50, –8, 0	–36, –26, 14	–44, –24, 4	–	–54, 2, 2	–60, –42, 14	–	–	–
	R	60, –14, –2	38, –30, 4	60, –10, 10	–	–	–	–	–	64, –36, 18
Thalamus	L	–12, –18, 4	–10, –20, 2	–4, –20, 0	–	–	–	–	–	–
Anterior cingulum	L	–2, –10, 40	–	–	–6, 2, 30	–	–	–	–4, 38, 2	–
	R	6, –16, 48	16, –12, 40	12, 46, 6	10, –4, 34	16, 38, 24	14, 42, 2	–	–	–
Caudate nucleus	L	–	–6, 8, –2	–12, 18, –2	–	–	–	–	–	–
	R	14, 12, –2	12, 18, 0	14, 12, –12	–	12, 8, –8	18, 20, 0	–	–	–
Putamen	R	–	30, 12, 0	–	–	–	–	–	–	–
MTG	L	–46, –22, –1	–56, –8, –16	–52, –2, –14	–	–52, –52, 14	–58, –6, –10	–	–	–
	R	64, –2, –16	70, –30, –8	56, –14, –8	–	–	60, –10, –14	–	–	50, –70, 0
Amygdala	L	–	–	–18, 6, –14	–22, –6, –10	–	–	–	–	–
	R	–	–	14, 6, –10	18, 0, –10	–	–	–	–	–
Insula	L	–34, 8, 4	–32, 12, –10	–	–28, 16, –8	–	–34, 6, 4	–	–	–
MOG	L	–	–	–	–	–	–	–	–	–48, –78, 12
Cerebellum	R	–	–	–	–	–	–	–	–	38, –64, –24
SPL	R	–	–	–	–	–	–	–	–	30, –76, 54

R right, *L* left, *SFG* superior frontal gyrus, *IFG* inferior frontal gyrus, *STG* superior temporal gyrus, *MTG* middle temporal gyrus, *MOG* middle occipital gyrus, *SPL* superior parietal lobule

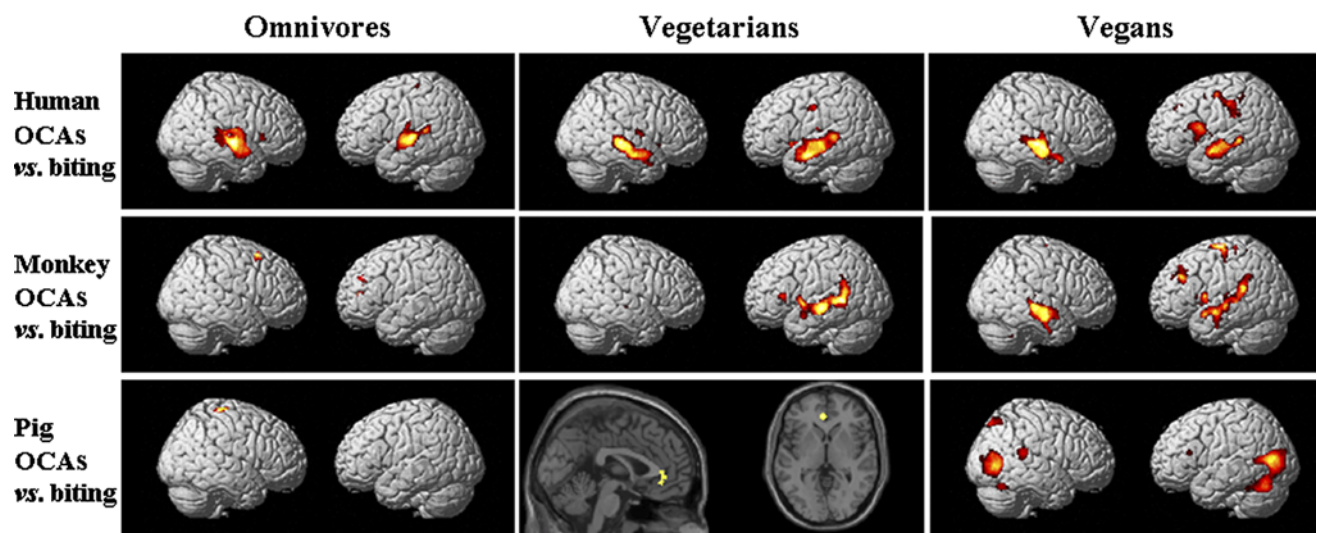


Fig. 2 Cortical activations on a rendered brain from omnivore, vegetarian and vegan subjects during the comparison of oral communicative actions (OCAs) versus biting by a human, a monkey,

and a pig (within-group analysis, two-sample t tests, $p < 0.05$ corrected for multiple comparisons). Images are in neurological convention

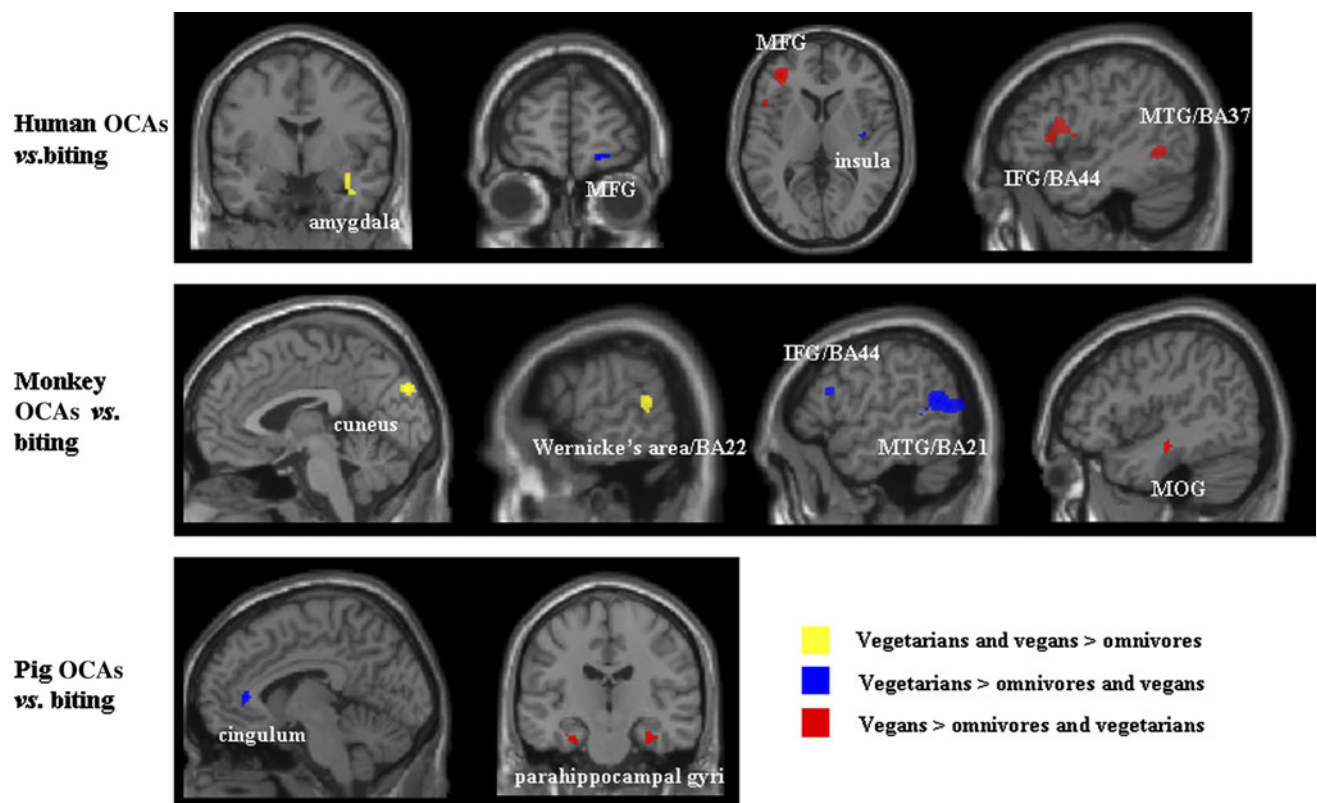


Fig. 3 Results of the between-group comparisons of oral communicative actions (OCAs) versus biting during “human/monkey/pig scenes” superimposed on a T1-weighted image in the Montreal Neurological Institute space. *Yellow* indicates areas activated in vegetarians and vegans versus omnivores. *Blue* indicates activations

specific to vegetarians. *Red* indicates activations specific to vegans. Images are presented in neurological convention. *MFG* middle frontal gyrus, *BA* Brodmann area, *IFG* inferior frontal gyrus, *MTG* middle temporal gyrus, *MOG* middle occipital gyrus

Table 6 Within-group comparisons (activation sites and Montreal Neurological Institute coordinates) of species-related recruitment during oral communicative actions in omnivores, vegetarians and vegans (ANOVA in each group, $p < 0.05$ family-wise error corrected)

Activation sites	Human versus monkey			Human versus pig			Monkey versus human		
	Omnivores	Vegetarians	Vegans	Omnivores	Vegetarians	Vegans	Omnivores	Vegetarians	Vegans
	L STG BA22 (Wernicke's area)/BA41	-50, -6, -6	-	-62, -24, 12	-66, -20, 4, -46, -36, 14	-	-	-	-
R STG (BA22)	66, -30, 14	58, -2, -12	-	52, -18, 2	-	-	-	-	-
L MTG	-48, -22, 0	-58, -18, -14	-66, -22, 2	-52, -48, 16	-54, -30, -10	-	-	-	-
R MTG (BA21)	-	60, -34, -6	52, -32, 2	64, -4, -20	70, -38, -6	60, -12, -12	-	-	-
R temporal pole	-	-	-	-	-	-	-	-	-
L SFG	-	-	-	-	-	-	-14, 52, 18	-	-
R SFG (BA8)	-	-	-	-	-	-	-	-	28, 28, 54
R MFG	-	-	-	-	-	-	-	-	-
L IFG (BA45)	-	-	-48, 22, 16	-38, 22, 22	-	-52, 12, 16	-	-38, 24, 16	-
R IFG (BA45)	48, 34, 0	60, 22, 2	-	58, 18, 8	-	-	-	-	-
R precentral gyrus	-	-	60, 8, 24	-	-	-	-	-	-
Cingulum	-	-	-	-	-	-	-	-	-4, -44, 44
L precuneus (BA7)	-	-	-	-	-	-	-	-	0, -60, 44
L SPL	-	-	-	-	-	-	-	-	-
R SPL	-	-	-	-	-	-	-	-	-
L insula	-	-30, 14, 2	-	-	-26, 10, 8	-	-	-	-
R insula	-	-	52, 12, 0	36, 30, 6	-	-	-	-	-
L supramarginal gyrus (BA48)	-	-	-54, -40, 30	-	-	-	-	-	-
L thalamus	-16, -10, 4	-	-	-10, -12, 0	-10, -14, 16	-20, 6, -8	-	-	-
R thalamus	-	8, -8, 16	-	-	30, 6, -4	-	-	-	-
R pallidus	26, -2, -2	-	-	-	-	-	-	-44, -72, 0	-
L IOG	-26, -100, -12	-	-	-	-	-	-	44, -74, -4	46, -70, -2
R IOG	30, -100, -8	-	-	-	-	-	8, -96, 14	8, -82, 26	12, -88, 26
R cuneus	-	-	-	-	-	-	-	-	20, -82, 0
R lingual gyrus	-	-	-	-	-	-	-6, -106, 4	-	-12, -96, 4
L SOL	-	-	-	-	-	-	-	-	-44, -68, -50
L cerebellum	-6, -80, -38	-	-	-	-	-12, -80, -42	-	-	-
R cerebellum	-	-	-	-	-	28, -64, -48	-	-	-
R amygdala	-	-	-	-	32, -2, -26	-	-	-	-

Table 6 continued

Activation sites	Pig versus human			Monkey versus pig			Pig versus monkey		
	Omnivores			Omnivores			Omnivores		
	Vegetarians	Vegans		Vegetarians	Vegans		Vegetarians	Vegans	
L STG BA22 (Wernicke's area)/BA41	-	-	-	-	-	-	-	-	-
R STG (BA22)	-	-	-	40, -30, 2	-	-	-	-	-
L MTG	-	-	-	-50, -32, -4	-	-	-	-	-
R MTG (BA21)	-	-	-	-	70, -28, -2	-	-	-	-
R temporal pole	-	-	-	50, 16, -38	-38, 8, -36	-	-	-	-
L SFG	-	-	-	-14, 54, 16	-	-	-	-	-
R SFG (BA8)	-	-	-	18, 18, 58	-	-	-	-	-
R MFG	-	-	-	32, 30, 32	46, 22, 44	-	-	-	-
L IFG (BA45)	-	-	-	-	-	-	-	-	-
R IFG (BA45)	-	-	-	-	-	-	-	-	-
R precentral gyrus	-	-	-	-	-	-	-	-	-
Cingulum	-	-	-	-12, 2, 34	-	-	-	-	-
L precuneus (BA7)	-	-	-	-	-	-	-	-	-
L SPL	-24, -64, 44	-	-	-	-	-	-32, -66, 52	-	-
R SPL	18, -86, 42	-	-	-	-	-	38, -50, 60	28, -78, 38	-
L insula	-	-	-	-	-	-	-	-	-
R insula	-	-	-	-	-	-	-	-	-
L supramarginal gyrus (BA48)	-	-	-	-	-	-	-	-	-
L thalamus	-	-	-	-	-	-	-	-	-
R thalamus	-	-	-	-	-	-	-	-	-
R pallidus	-	-	-	24, 18, -10	-	-	-	-	-
L IOG	-50, -70, -16	-26, -92, 12	-42, -78, 2	-	-	-	-52, -70, -12	-36, -94, -10	-24, -98, -6
R IOG	48, -70, -12	34, -88, -10	46, -72, -12	54, -22, -18	-	-	38, -90, -6	38, -88, 0	26, -92, 8
R cuneus	-	-	-	-	-	-	-	-	-
R lingual gyrus	-	-	-	-	-	-	-	-	-
L SOL	-	-	-	-8, -102, 12	-12, -102, 18	-10, -100, 6	-	-	-
L cerebellum	-	-	-	-	-	-14, -76, -40	-	-	-
R cerebellum	-	-	-	-	-	-	-	-	-
R amygdala	-	-	-	-	-	28, -76, -46	-	-	-
							28, -2, -16		

R right, L left, BA Brodmann area, STG superior temporal gyrus, MTG middle temporal gyrus, IOG inferior frontal gyrus, IFG inferior frontal gyrus, IOG inferior occipital gyrus, SOL superior occipital lobule, SFG superior frontal gyrus, SPL superior parietal lobule, MFG middle frontal gyrus

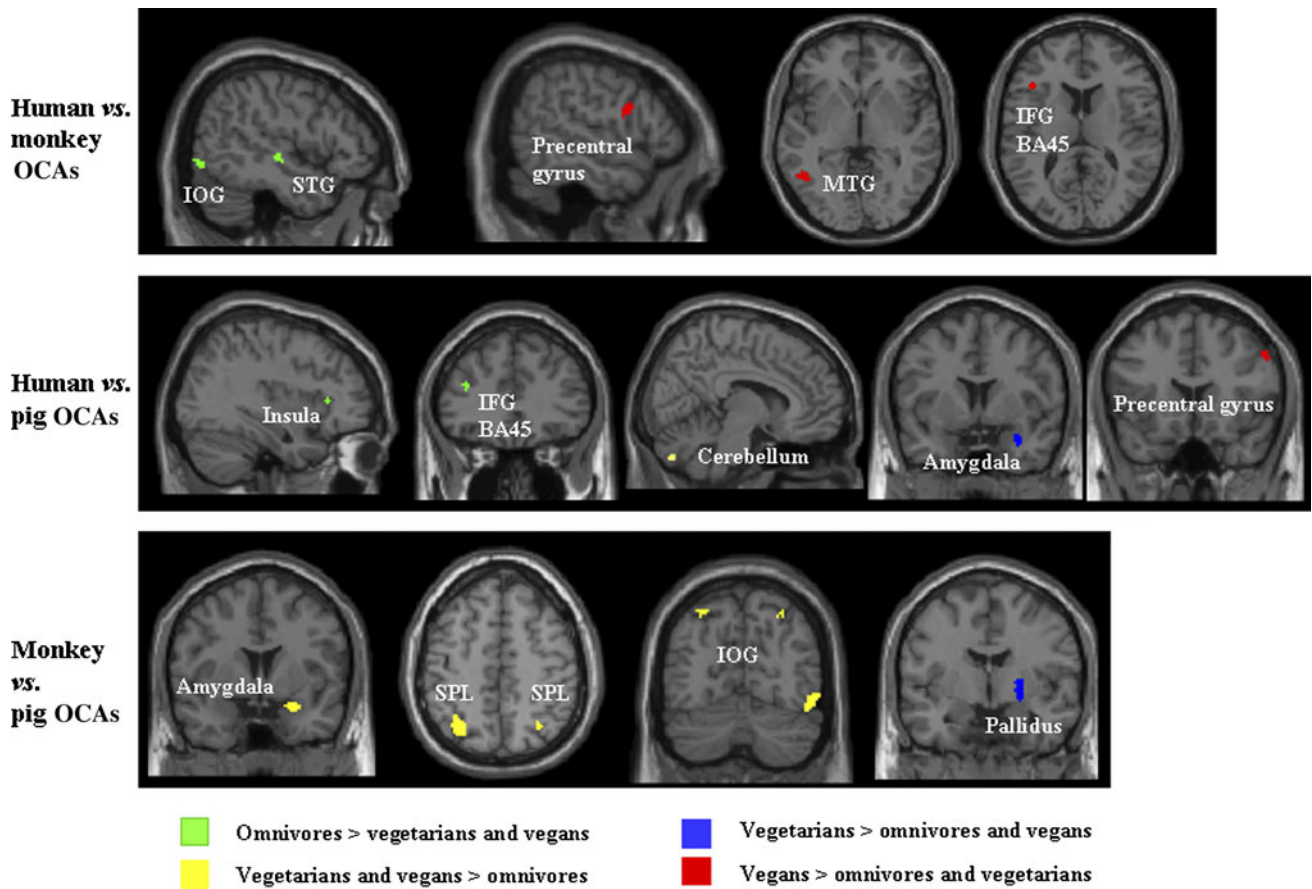


Fig. 4 Results of the between-species comparisons of oral communicative actions (OCAs) among omnivores, vegetarians, and vegans, superimposed on a T1-weighted image in the Montreal Neurological Institute space (between-group analysis, ANOVA, $p < 0.05$ corrected for multiple comparisons). *Green* indicates areas activated in omnivores versus vegetarians and vegans. *Yellow* indicates areas

activated in vegetarians and vegans versus omnivores. *Blue* indicates activations specific to vegetarians. *Red* indicates activations specific to vegans. Images are presented in neurological convention. *IOG* inferior occipital gyrus, *STG* superior temporal gyrus, *MTG* middle temporal gyrus, *BA* Brodmann area, *IFG* inferior frontal gyrus, *SPL* superior parietal lobule

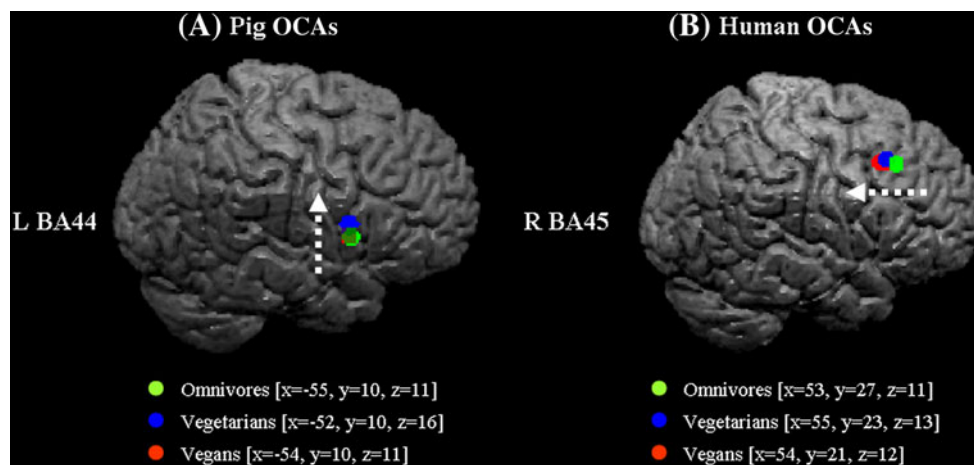


Fig. 5 Average activations (Montreal Neurological Institute coordinates in brackets), overlaid on a rendered template brain, of the: **a** left BA44 during the pig oral communicative actions (OCAs) condition, and **b** right BA45 during the human OCA condition in omnivores (*green*), vegetarians (*blue*) and vegans (*red*). In **a**, a cranial shift

(*arrow*) of the center of activation of the BA44 in vegetarians versus omnivores and vegans can be noted. In **b**, a posterior shift (*arrow*) of the center of activations of BA45 in vegetarian and vegans versus omnivores can be noted. *BA* Brodmann area

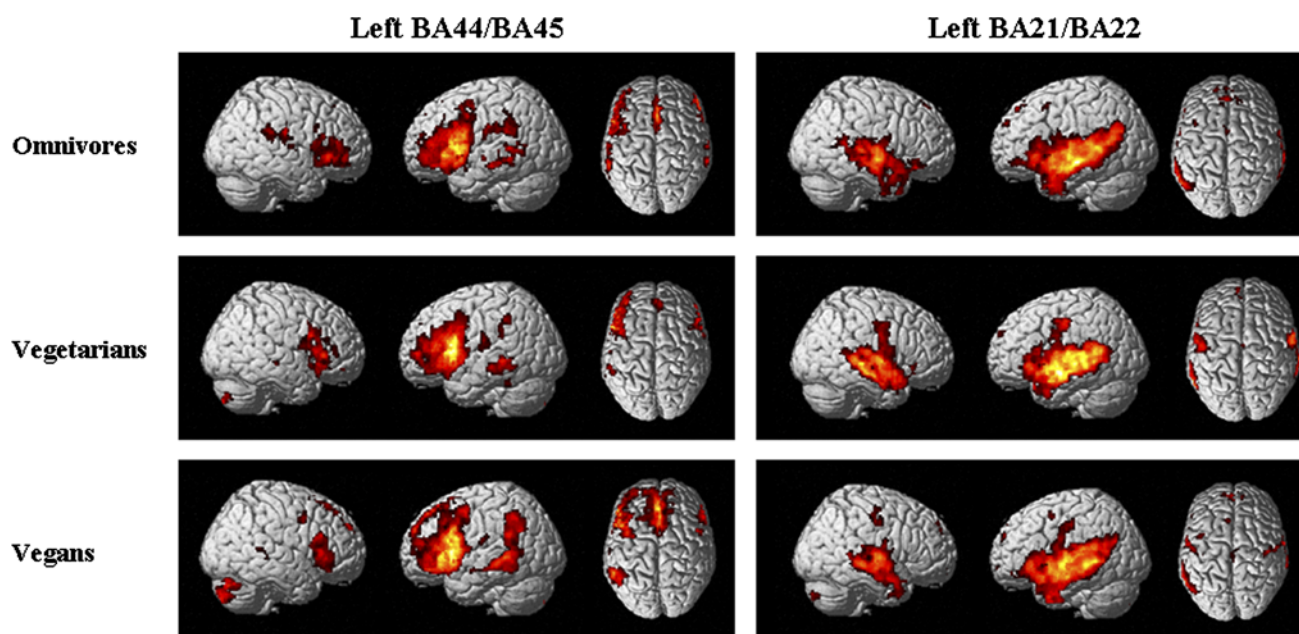


Fig. 6 Functional connectivity analysis showing the positive correlations between the left BA44/BA45 (*left panel*) and the left BA21/BA22 (*right panel*) and all the other brain voxels in omnivores (*top*

row), vegetarians (*middle row*) and vegans (*bottom row*) (within-group analysis, one-sample t test, $p < 0.05$ corrected for multiple comparisons). Images are in neurological convention

MTG, whereas vegans had a selective increased FC with the bilateral superior frontal gyrus (SFG), SMA, and the left parahippocampal gyrus (Fig. 7).

Discussion

In this study, we wished to map the central representation of mouth actions performed by humans and by other species in individuals with different dietary habits. To answer our first question (i.e., does processing of mouth actions performed by distinct species differ between vegetarians and vegans vs. omnivores?), since speech processing is a key aspect of social interactions, we compared observation of OCAs and biting by humans, monkeys and pigs within and between the three study groups. In contrast to OCAs, biting was associated with an increased activation of several regions in the temporo-occipital lobes, the parietal lobes and the cerebellum. Conversely, in contrast to biting, OCAs resulted in increased activity of several regions along the middle and superior temporal cortices, and the IFG with a different expression in the three study groups. Several neurophysiologic and imaging studies have mapped mouth actions along the superior temporal sulcus (STS) region, which includes the surface of the STG and MTG (Allison et al. 2000). The STS is involved in several functions, including theory of mind, audiovisual integration, motion perception, speech processing and perception of faces (Hein and Knight 2008). A review of foci of activations within this region reported in several fMRI

studies has led to the identification of an anterior portion, mainly involved in speech processing, and a posterior one, mainly recruited by cognitive demands (Hein and Knight 2008). These results argue against distinct functional subregions in the STS and favor the hypothesis that the same STS region can serve different cognitive functions as a flexible component in networks with other brain regions. In line with this, the foci of activations we found at the between-group comparisons were rather heterogeneous in terms of coordinates and laterality. The left pars opercularis of the IFG contains a representation of mouth actions performed by humans (Buccino et al. 2001). Recruitment of this region, together with regions located in the parietal and temporal lobes, contributes to the understanding of actions performed by others by transcoding the observed action into a corresponding motor plan (Rizzolatti et al. 2001), a mechanism which is critical for social interactions. During “human scenes”, the comparison of OCAs versus biting showed an increased activity of the right amygdala in vegetarians and vegans versus omnivores. The amygdala contributes to the analysis of body movements for perception of actions through its connections with the STS and the frontal cortex (Allison et al. 2000), thus adding emotional salience to sensory inputs. Therefore, its increased activity in vegetarians and vegans suggests a different analysis of dispositions and intentions of other people in these individuals.

To answer our second question (i.e., do functional architecture differences exist between vegetarians and vegans?), regions of specific activations in each group were

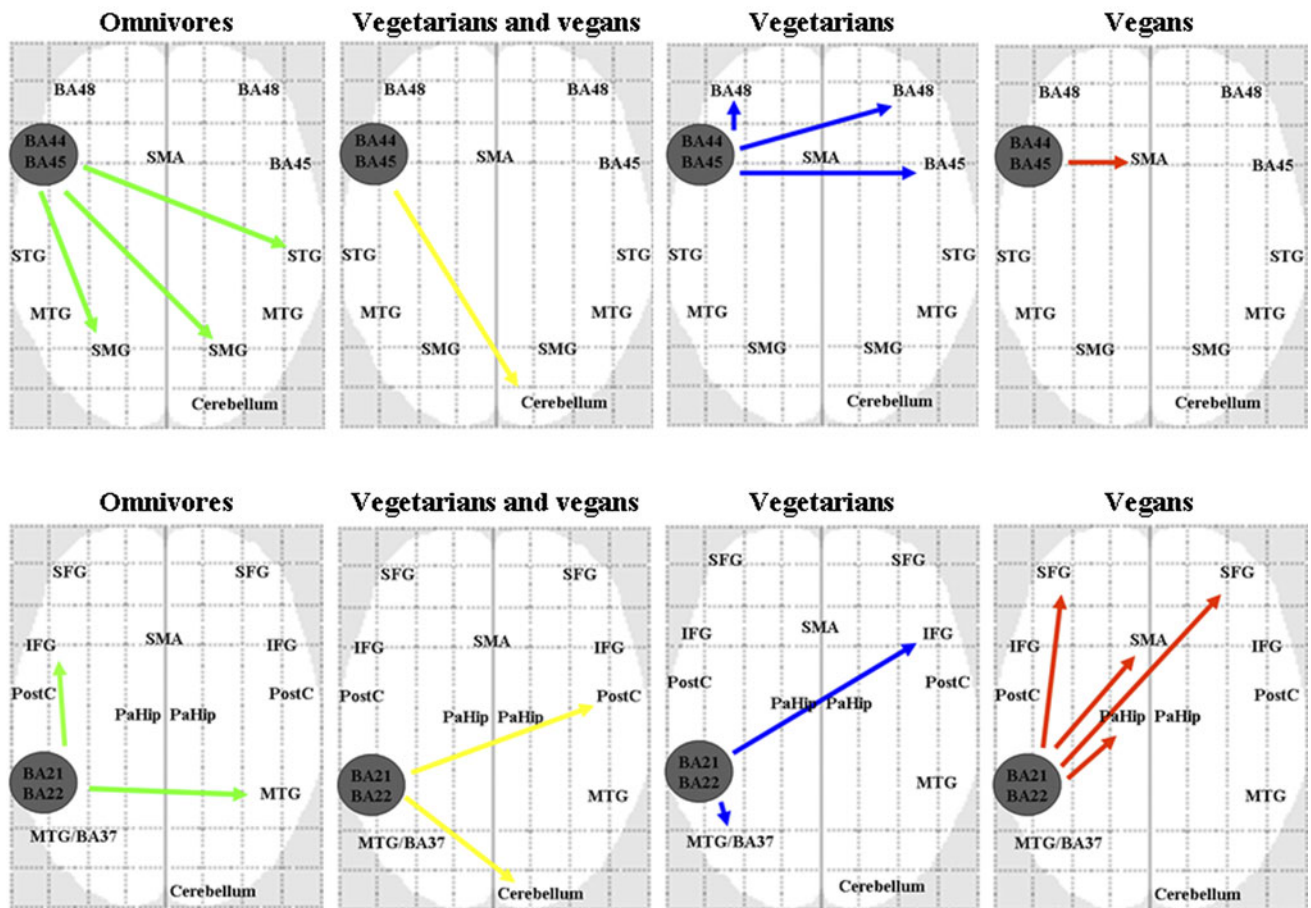


Fig. 7 Schematic representation and summary of between-group comparisons of functional connectivity strength with the left BA44/BA45 (top row) and left BA 21/22 (bottom row). Green indicates connection strengths higher in omnivores versus vegetarians and vegans. Yellow indicates connection strengths higher in vegetarians and vegans versus omnivores. Blue indicates connections specific to

vegetarians. Red indicates connections specific to vegans. BA Brodmann area, SMG supramarginal gyrus, STG superior temporal gyrus, SMA supplementary motor area, MTG middle temporal gyrus, postC postcentral gyrus, IFG inferior frontal gyrus, SFG superior frontal gyrus, PaHip parahippocampal gyrus

further investigated. Compared to the other two groups, vegetarians showed a selective increased recruitment of the right MFG and right posterior insula, whereas vegans recruited selectively the left MFG, IFG (pars opercularis) and MTG (posterior portion). The MFG contributes to social cognitive processes (such as making inferences of others and social perception) (Murty et al. 2010). Recent meta-analyses have shown that the insula can be consistently parcellated in an anterior and a posterior portion (Cauda et al. 2012; Chang et al. 2012). The anterior insula is mostly activated by cognition, whereas the posterior is mostly activated by interoception, perception and emotion (Cauda et al. 2012). The insula also modulates connections between the MNS and the limbic system in social mirroring and in the ability to empathize with others (Iacoboni 2009). The left IFG and posterior portion of the MTG are part of the MNS. Such a system includes Broca's area, which is

involved in language processing in humans. Collectively, these results indicate that different portions of the empathy-related networks contribute to the modulation of social interactions with other individuals in vegetarians and vegans compared to omnivores. Our previous investigation (Filippi et al. 2010) showed a higher empathy in vegetarians and vegans versus omnivores. Combined with the present results, these findings support the theory (Thompson and Gullone 2003) that subjects with a high level of empathy towards animals might have a more general capacity for empathy and related prosocial behaviors, and identify a possible biological substrate for such a theory.

The analysis of “animal scenes” provided some additional stimulating results. During “monkey scenes”, compared to omnivores, vegetarians and vegans had increased activity of the bilateral cuneus and left MTG, in a region that roughly corresponds to the location of Wernicke's

area. In addition, vegetarians selectively activated the left MTG and IFG (pars opercularis), and vegans the right MTG and MOG. All these areas are recruited consistently in healthy individuals during lipreading, to different extents according to the language task used (Paulesu et al. 2003). The increased recruitment of Wernicke's area and cuneus in vegetarians and vegans might be secondary to their attempt to decode monkey mouth gesture. More critically, vegetarians had a preferential recruitment of the left pars opercularis of the IFG, which suggests an additional process of matching mouth action of the monkey with that of the viewer, whereas vegans engaged associative temporo-occipital areas in the right hemisphere, suggesting a role of higher cognitive processes involved in sentence comprehension (Just et al. 1996).

The comparison of OCA versus biting in "pig scenes" also detected particular patterns of recruitment in vegetarians and vegans. Specifically, vegetarians showed a selective increased activity of the anterior cingulum, which likely reflects a strong empathic response (Devinsky et al. 1995; Phan et al. 2002) or simply an enhanced attention (Singer et al. 2004), whereas vegans activated the bilateral parahippocampal gyrus, which has a role in auditory-verbal memory functions (Grasby et al. 1993) and, through its connections with the amygdala, contributes to emotion-driven learning (Murty et al. 2010).

To address our third question (i.e., does processing of mouth actions differ according to the species involved and their phylogenetic proximity to humans?), we limited the analysis to OCAs, since they represent the basis of intra- and inter-group relationships in humans. During human versus monkey OCAs, compared to vegetarians and vegans, omnivores had an increased activity of part of the visual areas of the observation-execution matching system. Vegans had selective increased activity of the left MTG and the frontal portion of the system, further supporting the notion of increased recruitment of regions of the MNS in these subjects. Consistent with the role of the anterior portion of the insula in interpersonal interactions, this region was more active, in combination with the left IFG, in omnivores compared to vegetarians and vegans during human versus pig OCAs. Additional between-group differences in processing human versus pig actions concerned areas involved in empathy processing, including the amygdala and the anterior lobe of the cerebellum. This latter region plays a crucial role in motor learning and language processing as demonstrated by a recent meta-analysis (Jirak et al. 2010). Importantly, between-group differences in processing monkey versus pig OCAs revealed activity of areas that have a role in spatial attention, such as the SPL and IOG in vegetarians and vegans, as well as the globus pallidus in vegetarians. Overall, these findings support the notion that, despite

vegetarians and vegans showing a particular pattern of recruitment of regions that are part of the MNS during processing mouth actions executed by other animals, the activity of this system remains higher when they are dealing with actions performed by their conspecifics, probably as a consequence of the matching of the observed human action with their motor repertoire, as part of a common representational format. In addition, species proximity with humans can modulate MNS recruitment in these subjects, as suggested by the between-group differences observed for monkey, but not pig OCAs.

Complementing the analysis of activations, the analysis of FC detected striking between-group differences in the strengths of connections with the cerebellum (which was highly significantly connected in vegetarians and vegans vs. omnivores) and the SMA (which had a selective higher connectivity in vegans). Remarkably, the connectivity of these two areas was not influenced by the seed-regions (IFG or STS) used to run the analysis, type of task, or stimulus. Despite the fact that activation of these two areas has been reported in several studies investigating the MNS, their role, in the context of MNS and empathy theories, has been neglected by the majority of researchers. The analysis of single-subject data has recently led to the identification of a series of brain areas involved in action observation and execution (Gazzola and Keysers 2009), which extends beyond the original MNS and also includes the cerebellum and SMA. Within the framework of this model of action observation and execution, such brain regions cooperate in forward and inverse internal models to associate other people's actions with their own actions and sensations. In particular, while the cerebellum, through its connections to the premotor and cingulate cortices, provides a motor and somatosensory representation of others' actions and contributes to predicting actions, the SMA serves as a gatekeeper of premotor activity of the primary motor cortex, thus determining motor behaviour (Gazzola and Keysers 2009).

Collectively, our results reveal that distinct brain responses are evoked by mouth actions performed by different species in people with vegetarian and vegan eating habits, and there are differences between vegetarians and vegans, supporting the role of the action observation execution matching system in social cognition, enabling us to communicate and interact with our conspecifics and also with species in phylogenetic proximity to humans.

Acknowledgments The authors are grateful to Prof. Paul M. Matthews (Department of Clinical Neurosciences, Imperial College London, and GSK Clinical Imaging Centre, Hammersmith Hospital, London, UK) and Dr. Mark A. Horsfield (Department of Cardiovascular Sciences, University of Leicester, Leicester, UK) for their thoughtful comments to the manuscript.

Conflict of interest The authors have no commercial interests with regard to the study reported in the present manuscript.

References

- Allison T, Puce A, McCarthy G (2000) Social perception from visual cues: role of the STS region. *Trends Cogn Sci* 4:267–278
- Biswal B, Yetkin FZ, Haughton VM, Hyde JS (1995) Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magn Reson Med* 34:537–541
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 13:400–404
- Buccino G, Lui F, Canessa N, Patteri I, Lagravinese G, Benuzzi F, Porro CA, Rizzolatti G (2004) Neural circuits involved in the recognition of actions performed by nonconspecifics: an FMRI study. *J Cogn Neurosci* 16:114–126
- Cauda F, Costa T, Torta DM, Sacco K, D'Agata F, Duca S, Geminiani G, Fox PT, Vercelli A (2012) Meta-analytic clustering of the insular cortex: characterizing the meta-analytic connectivity of the insula when involved in active tasks. *Neuroimage* 62:343–355
- Chang LJ, Yarkoni T, Khaw MW, Sanfey AG (2012) Decoding the role of the insula in human cognition: functional parcellation and large-scale reverse inference. *Cereb Cortex*
- Cheng Y, Lin CP, Liu HL, Hsu YY, Lim KE, Hung D, Decety J (2007) Expertise modulates the perception of pain in others. *Curr Biol* 17:1708–1713
- Devinsky O, Morrell MJ, Vogt BA (1995) Contributions of anterior cingulate cortex to behaviour. *Brain* 118(Pt 1):279–306
- Filippi M, Riccitelli G, Falini A, Di Salle F, Vuilleumier P, Comi G, Rocca MA (2010) The brain functional networks associated to human and animal suffering differ among omnivores, vegetarians and vegans. *PLoS ONE* 5:e10847
- Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005) The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proc Natl Acad Sci USA* 102:9673–9678
- Friston KJ, Holmes AP, Poline JB, Grasby PJ, Williams SC, Frackowiak RS, Turner R (1995) Analysis of fMRI time-series revisited. *Neuroimage* 2:45–53
- Friston KJ, Holmes AP, Price CJ, Buchel C, Worsley KJ (1999) Multisubject fMRI studies and conjunction analyses. *Neuroimage* 10:385–396
- Friston KJ, Penny WD, Glaser DE (2005) Conjunction revisited. *Neuroimage* 25:661–667
- Gazzola V, Keysers C (2009) The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb Cortex* 19:1239–1255
- Grasby PM, Frith CD, Friston KJ, Bench C, Frackowiak RS, Dolan RJ (1993) Functional mapping of brain areas implicated in auditory-verbal memory function. *Brain* 116(Pt 1):1–20
- Hein G, Knight RT (2008) Superior temporal sulcus—It's my area: or is it? *J Cogn Neurosci* 20:2125–2136
- Iacoboni M (2009) Imitation, empathy, and mirror neurons. *Annu Rev Psychol* 60:653–670
- Jirak D, Menz MM, Buccino G, Borghi AM, Binkofski F (2010) Grasping language—a short story on embodiment. *Conscious Cogn* 19:711–720
- Just MA, Carpenter PA, Keller TA, Eddy WF, Thulborn KR (1996) Brain activation modulated by sentence comprehension. *Science* 274:114–116
- Lancaster JL, Woldorff MG, Parsons LM, Liotti M, Freitas CS, Rainey L, Kochunov PV, Nickerson D, Mikiten SA, Fox PT (2000) Automated Talairach atlas labels for functional brain mapping. *Hum Brain Mapp* 10:120–131
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage* 19:1233–1239
- Murty VP, Ritchey M, Adcock RA, LaBar KS (2010) fMRI studies of successful emotional memory encoding: a quantitative meta-analysis. *Neuropsychologia* 48:3459–3469
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9:97–113
- Paulesu E, Perani D, Blasi V, Silani G, Borghese NA, De Giovanni U, Sensolo S, Fazio F (2003) A functional-anatomical model for lipreading. *J Neurophysiol* 90:2005–2013
- Phan KL, Wager T, Taylor SF, Liberzon I (2002) Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage* 16:331–348
- Regan T (1985) The case for animal rights. University of California, Berkeley 422
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2:661–670
- Shamay-Tsoory SG (2011) The neural bases for empathy. *Neuroscientist* 17:18–24
- Shamay-Tsoory SG, Aharon-Peretz J, Perry D (2009) Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain* 132:617–627
- Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD (2004) Empathy for pain involves the affective but not sensory components of pain. *Science* 303:1157–1162
- Singer T, Seymour B, O'Doherty JP, Stephan KE, Dolan RJ, Frith CD (2006) Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439:466–469
- Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D (2005) Listening to action-related sentences activates fronto-parietal motor circuits. *J Cogn Neurosci* 17:273–281
- Thompson KL, Gullone E (2003) Promotion of empathy and prosocial behaviour in children through humane education. *Australian Psychologist* 38:175–182
- Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M (2002) Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 15:273–289
- Xiang HD, Fonteijn HM, Norris DG, Hagoort P (2010) Topographical functional connectivity pattern in the perisylvian language networks. *Cereb Cortex* 20:549–560