

Neural Circuits Involved in the Recognition of Actions Performed by Nonconspecifics: An fMRI Study

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Abstract

■ Functional magnetic resonance imaging was used to assess the cortical areas active during the observation of mouth actions performed by humans and by individuals belonging to other species (monkey and dog). Two types of actions were presented: biting and oral communicative actions (speech reading, lip-smacking, barking). As a control, static images of the same actions were shown. Observation of biting, regardless of the species of the individual performing the action, determined two activation foci (one rostral and one caudal) in the inferior parietal lobule and an activation of the pars opercularis of the inferior frontal gyrus and the adjacent ventral premotor cortex. The left rostral parietal focus (possibly BA 40) and the left premotor focus were very similar in all three conditions, while the right side foci were stronger during the observation of actions made by conspecifics. The observation of speech reading activated the left

pars opercularis of the inferior frontal gyrus, the observation of lip-smacking activated a small focus in the pars opercularis bilaterally, and the observation of barking did not produce any activation in the frontal lobe. Observation of all types of mouth actions induced activation of extrastriate occipital areas. These results suggest that actions made by other individuals may be recognized through different mechanisms. Actions belonging to the motor repertoire of the observer (e.g., biting and speech reading) are mapped on the observer's motor system. Actions that do not belong to this repertoire (e.g., barking) are essentially recognized based on their visual properties. We propose that when the motor representation of the observed action is activated, the observer gains knowledge of the observed action in a "personal" perspective, while this perspective is lacking when there is no motor activation. ■

INTRODUCTION

Understanding actions made by others is a fundamental cognitive function on which social life and the survival of individuals depend. However, in spite of its importance, the neural mechanisms underlying action recognition are largely unknown. Recently, it has been proposed that at the basis of action recognition is a sensorimotor matching mechanism. According to this view, the observed actions, coded in the temporal lobe, are directly matched to the motor representation of the same actions. Since the motor representation of the observing individual is activated, the meaning of the observed actions is understood (see Rizzolatti, Fogassi, & Gallese, 2001).

Empirical evidence for the existence of a direct matching mechanism has been provided by the discovery of mirror neurons. These neurons, which were first found

in the monkey ventral premotor cortex (area F5), discharge both when the monkey performs a specific goal-directed action (e.g., grasping, tearing, holding) and when it observes another individual performing the same or a similar action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Rizzolatti, 1996; Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). More recently, mirror neurons were also described in the rostral part of the monkey inferior parietal lobule (area PF) (Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Fogassi et al., 1998).

Evidence that a mirror neuron system also exists in humans comes from transcranial magnetic stimulation (TMS), electroencephalographic (EEG), and magnetoencephalographic (MEG) studies and brain imaging experiments.

TMS studies demonstrated that the observation of hand actions made by another individual leads to an increase of motor-evoked potentials recorded from those same hand muscles that the observer uses when he/she performs the observed action (Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Gangitano, Mottaghy, & Pascual-Leone, 2001; Strafella & Paus, 2000; Fadiga,

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Fogassi, Pavesi, & Rizzolatti, 1995). This indicates that observing an action automatically evokes its motor representation in the observer.

A matching between observed and executed actions was demonstrated also by EEG and MEG studies. These studies showed that the rhythms, specific for the central (sensorimotor) region of cerebral cortex and that disappear during the execution of hand actions, also disappear (or significantly decrease) during the observation of hand actions (Cochin, Barthelemy, Roux, & Martineau, 1999; Hari et al., 1998).

While TMS and MEG/EEG data demonstrated the existence of a mirror neuron system in humans, they could not provide information on the neural circuits underlying it. Data on mirror neuron system localization were first obtained by positron emission tomography studies and, more recently, by functional magnetic resonance imaging (fMRI) experiments (Manthey, Schubotz, & von Cramon, 2003; Iacoboni et al., 1999, 2001; Grèzes, Costes, & Decety, 1998; Decety et al., 1997; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti, Fadiga, Matelli, et al., 1996). These brain imaging studies showed that the circuit selectively activated by the observation of actions made by others is formed by the cortex within the superior temporal sulcus (STS region), the inferior parietal lobule, and the pars opercularis of the inferior frontal gyrus plus the adjacent ventral area 6. This circuit closely corresponds to the circuit where, in the monkey, neurons were found that respond to the observation of biological actions (see Rizzolatti et al., 2001).

The above-mentioned brain imaging studies were all concerned with hand and arm movements. Recent fMRI experiments investigated, in addition to hand, mouth, and foot actions (Buccino et al., 2001). The results showed that the observation of mouth and foot actions also activates the frontal premotor areas and, in the case of transitive (goal-directed) actions, the inferior parietal lobule. The representations of the different actions are located in different sectors of the premotor cortex and inferior parietal lobule. In the frontal lobe, the activations due to the observation of actions made by the mouth, hand, and foot are somatotopically organized in a dorsoventral fashion and basically correspond to the motor representations of foot, hand, and mouth as classically described (Woolsey et al., 1952; Penfield & Rasmussen, 1950).

Prompted by these findings and in particular by the presence of clear activations related to mouth actions, we examined whether the observation of mouth actions made by nonconspecifics (monkey and dog) would activate the same cortical areas in humans that are active during the observation of human mouth actions. To study this, we presented normal human volunteers with two kinds of actions: biting and oral communicative actions. Actions were performed by a man, a monkey, and a dog. Our goal was to learn whether an individual

recognizes actions performed by nonconspecifics using the same cortical circuits involved in the recognition of actions made by human beings.

RESULTS

Figure 1 shows the activations related to the observation of biting made by a man, a monkey, and a dog. Stimuli used in the experiment are illustrated in Figure 2 that shows frames from action sequences presented to the subjects during the experiment.

For all three types of stimuli (man, monkey, and dog biting actions), there was an activation of visual occipital areas and, most interestingly, of the parietal and premotor cortex, bilaterally.

The parietal activations were located in the inferior parietal lobule. Two distinct activation foci were observed in the left hemisphere, one located rostrally and one caudally for all three types of stimuli. The same activation pattern was found in the right hemisphere during the observation of biting performed by a man and a monkey, whereas a single, caudal focus was present during biting made by a dog. The right activations were stronger during the observation of biting made by a man.

The premotor cortex activations during the observation of biting made by all three species lay virtually in the same sector of the left hemisphere, namely in the dorsal part of the pars opercularis of the inferior frontal gyrus and the immediately adjacent part of the ventral premotor cortex. The activation of the premotor cortex on the right side was located in the same premotor sector, but it was evident only during the observation of biting made by a man.

Figure 3 shows the activations found when subjects observed communicative actions made by a man (silent speech), a monkey (lip-smacking), and a dog (barking). The stimuli used are illustrated in Figure 4 that shows frames from action sequences presented to the subjects during the experiment.

The observation of speech movements determined a strong activation of the left pars opercularis of the inferior frontal gyrus, plus an activation of the rostral part of the inferior frontal gyrus (area orbitalis) on the same side. Activations on the right side were present, but very weak. No activations were found in the parietal lobe, while a clear activation was present bilaterally in the temporal lobe.

During the observation of the monkey communicative action (lip-smacking), there was a small bilateral activation of the pars opercularis of the inferior frontal gyrus. A small activation was present also in the right STS. Finally, during the observation of silent barking, there was only a small activation in the right STS. No activation was found in the frontal lobe.

During the observation of communicative actions made by all species, there was a strong activation of the occipital areas (Figure 3). It is worth noting that the

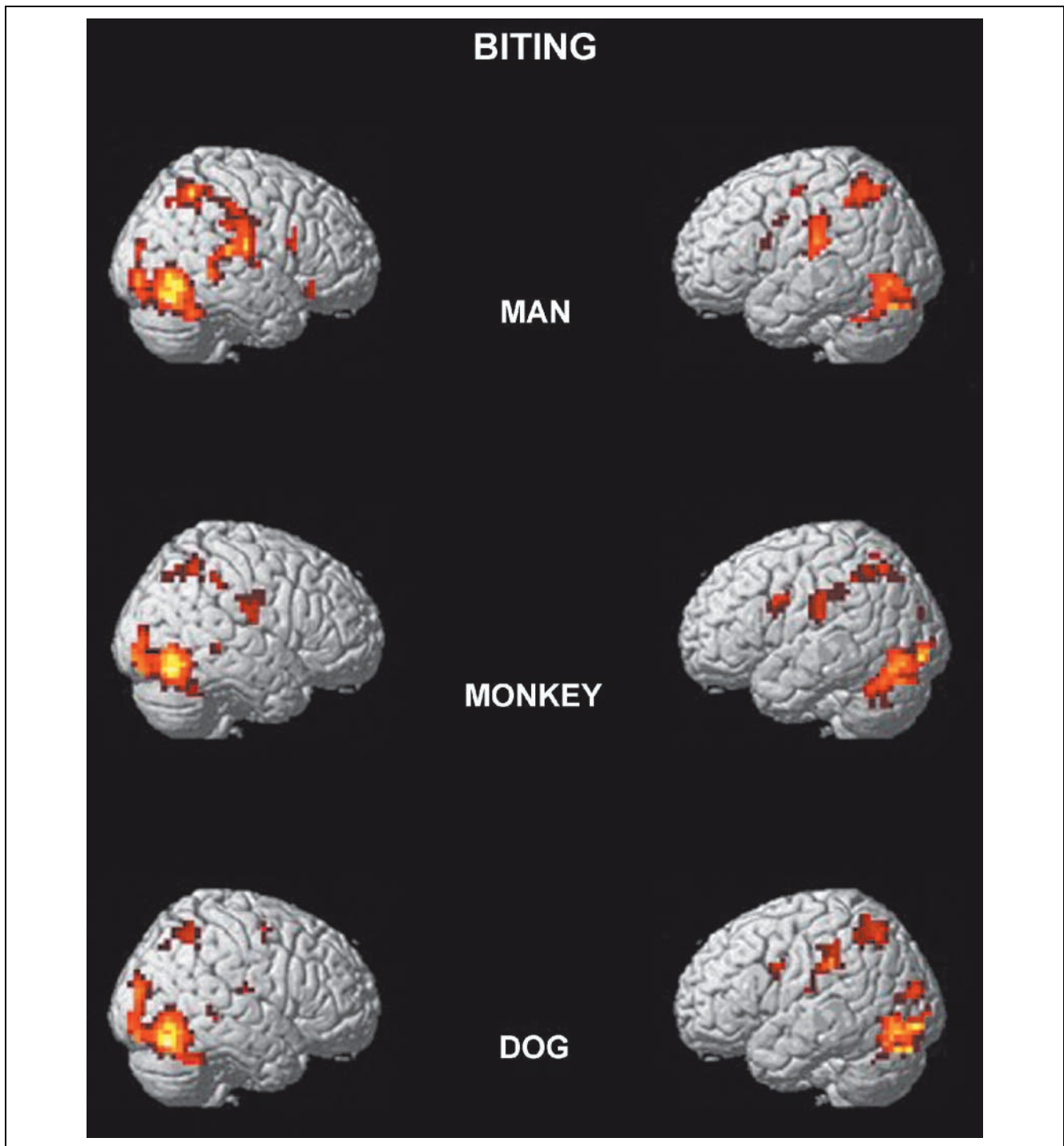


Figure 1. Cortical areas activated during the observation of biting performed by a man, a monkey, and a dog. MNI coordinates and the correspondent TAL coordinates of the activated foci are reported in Table 1.

weakest occipital activations were present during speech reading.

Tables 1 and 2 indicate the local maxima of the active areas in all conditions referred to the standard Montreal Neurological Institute Brain (MNI) and to Talairach space (TAL) (Talairach & Tournoux, 1988).

Direct comparison of time series of the BOLD signal of active conditions (after baseline subtraction) in all com-

municative actions in left pars opercularis of the inferior frontal gyrus (BA 44 as defined by Amunts et al., 1999; precise stereotaxic coordinates can be found at www.fz-juelich.de) showed that there was a significant difference between the observation of silent speech versus the observation of lip-smacking, mean: 0.180, $t(13) = 3.4$, $p < .002$, and the observation of barking, mean: 0.222, $t(13) = 4.7$, $p < .0002$. No difference was present in the

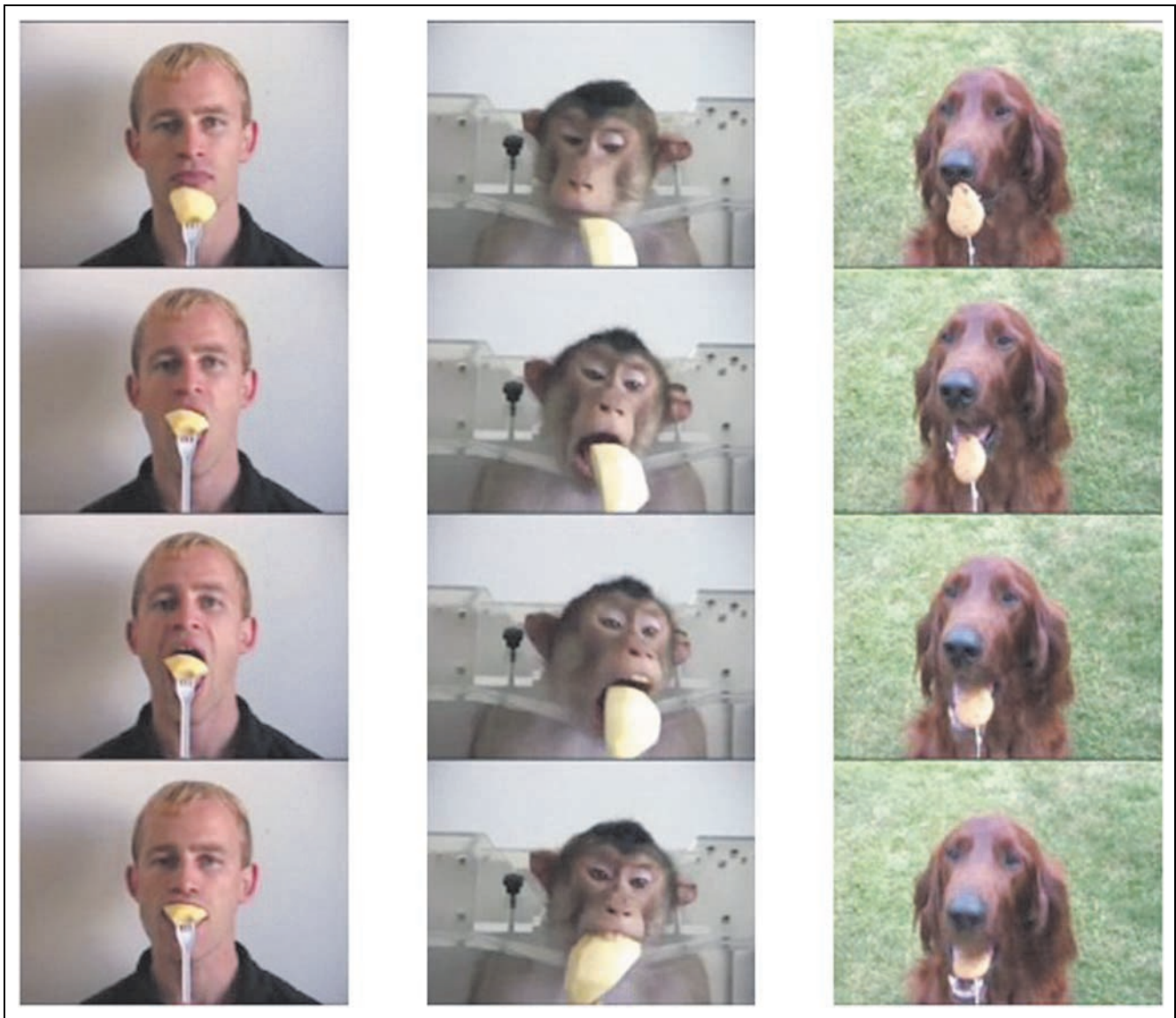


Figure 2. Selected frames from the video sequences showing biting made by a man, a monkey, and a dog used during the experiment.

comparison between the observation of lip-smacking versus the observation of barking, mean: 0.041, $t(13) = 0.72$, $p < .240$.

DISCUSSION

The aim of the present experiment was to assess whether the observation of actions performed by animals would activate the same brain areas that are active when subjects observe actions made by humans. The results showed that when the observed action is common to animals and humans, there is a clear overlap between the activated areas, in spite of the enormous differences in the visual aspects of the observed stimuli. In contrast, during the observation of actions that, like oral communicative actions, have a common goal, but are expressed differently in the

three species, there is a clear difference in the distribution and extent of activations.

Observation of Biting

Biting defines an action that consists in the nipping something with the teeth. Regardless of who is performing it, biting has a common visual aspect: the mouth moves toward an object, opens, and touches the object. Apart from this, biting made by a man, a monkey, and a dog is visually very different. Not only they differ in the visual appearance of the body part (head, face, and snout) performing the action, but also in how movements are made. In spite of this, the observation of biting made by the individuals of the three species determined a very similar activation pattern. In all cases, besides the visual occipital areas,

activations were present in the inferior parietal lobule and the premotor cortex.

The activations in the inferior parietal lobule were located in two distinct sectors: one rostral and one caudal. In the monkey, the rostral sector of the inferior parietal lobule (area PF) contains neurons responding to somatosensory, visual, or both somatosensory and visual stimuli. Many PF neurons discharge also during active

mouth and hand movements (Gallese et al., 2002; Fogassi et al., 1998; Leinonen, Hyvärinen, Nyman, & Linnankoski, 1979; Leinonen & Nyman, 1979). Most interestingly, recent data showed that part of the visually responsive neurons are active preferentially, or even exclusively, during the observation of biological actions and some have mirror properties (Gallese et al., 2002; Fogassi et al., 1998).

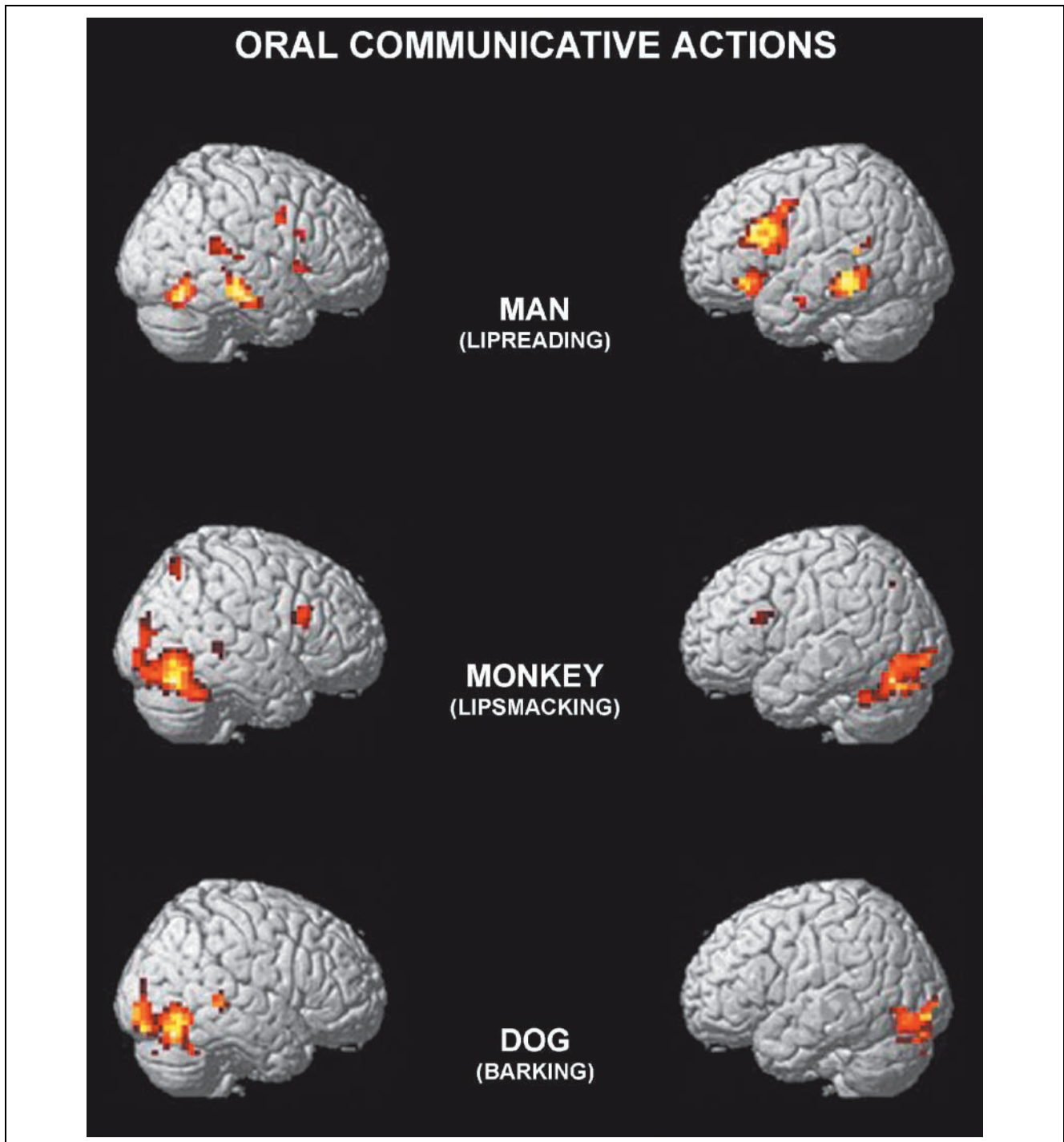


Figure 3. Cortical areas activated during the observation of oral communicative actions performed by a man (silent speech), a monkey (lip-smacking), and a dog (barking). MNI coordinates and the correspondent TAL coordinates of the activated foci are reported in Table 2.

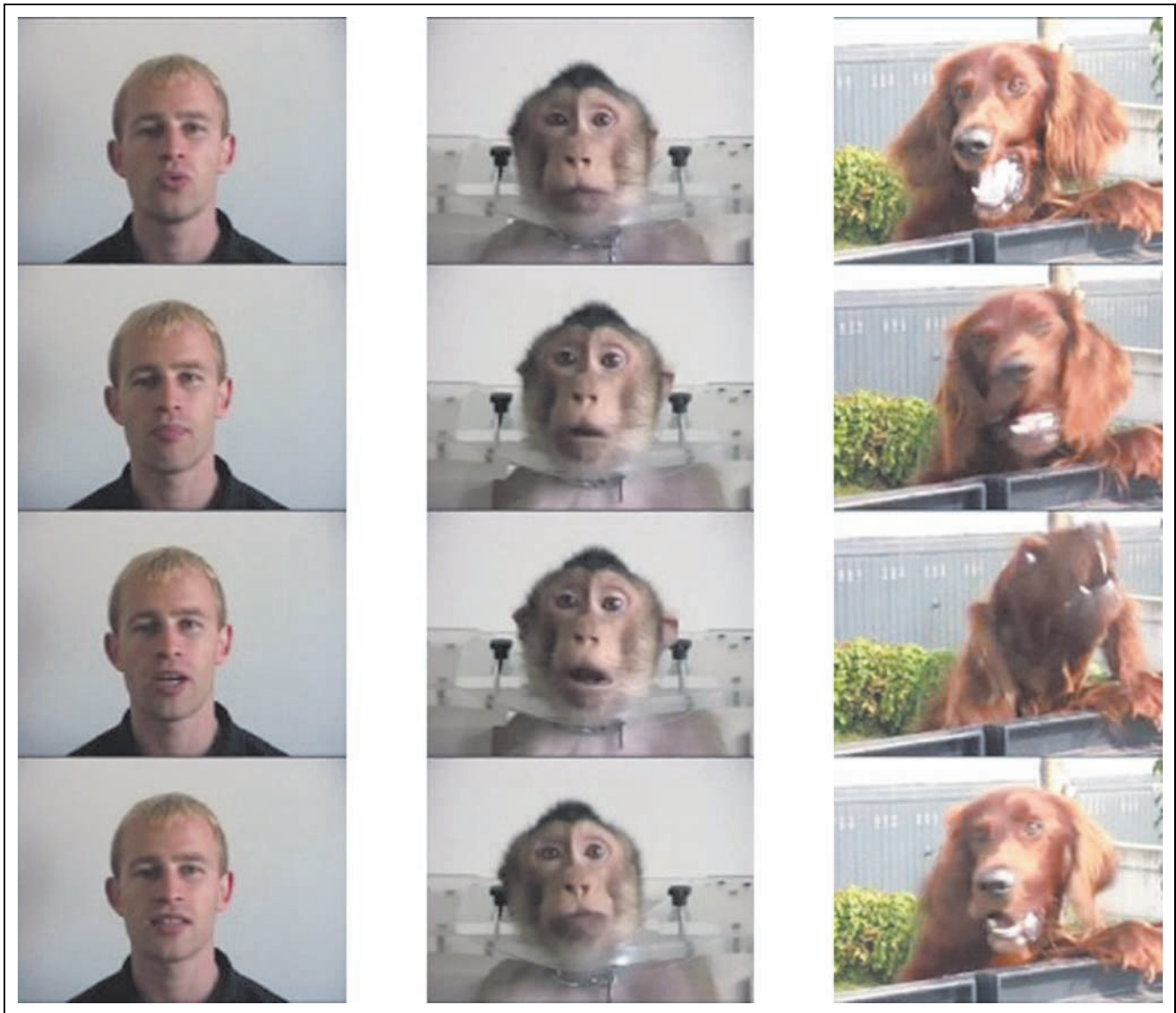


Figure 4. Selected frames from the video sequences showing oral communicative actions presented to the subjects during the experiment. Man = silent speech; monkey = lip-smacking; dog = barking.

In accord with monkey data, human brain imaging studies strongly suggest that a mirror neuron system is also present in the rostral sector of the inferior parietal lobule (area PF or BA 40). This sector is active during the observation of mouth and hand actions in the absence of any active movement (Buccino et al., 2001). Furthermore, area PF, together with the adjacent cortex inside the intraparietal sulcus (possibly the human anterior intraparietal), becomes active during the execution of actions such as object manipulation (Binkofski et al., 1999). The motor role of the rostral inferior parietal lobule in hand movements is confirmed by clinical studies showing that lesions centered on this region determine selective impairment of grasping (Binkofski et al., 1998).

The present data show that observation of biting made by nonconspecifics activates the same foci in the rostral

inferior parietal lobule as the observation of biting made by humans. The similarity in activation is particularly striking in the left hemisphere. In contrast, right parietal activation appears to be stronger during the observation of biting made by conspecifics. The activation intensity decreases when the individual performing the observed action belongs to a species more distant from the human one, dog biting producing the weakest activation.

It appears therefore that the left hemisphere codes the action meaning, abstracting it from the stimulus visual appearance, while the right hemisphere is tuned also to the stimulus-specific pictorial aspects. Because humans are much more exposed to actions of conspecifics than to those of nonconspecifics, one may postulate that human actions are more represented in the parietal lobe than those performed by animals.

Table 1. Cortical Cluster Related to the Observation of Biting Actions

<i>Anatomical Region</i>	<i>k</i>	<i>Z</i>	<i>Spatial Coordinates</i>					
			<i>MNI</i>			<i>TAL</i>		
			<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>
<i>Man</i>								
Inferior parietal lobule R	141	5.07	60	-16	20	59	-15	19
Inferior parietal lobule L	56	4.70	-60	-24	20	-59	-22	20
Inferior parietal lobule/intraparietal sulcus R	93	4.68	36	-52	52	36	-48	50
Inferior parietal lobule/intraparietal sulcus L	86	4.35	-32	-48	44	-32	-45	43
Inferior frontal gyrus, pars opercularis R	14	3.68	44	16	24	44	17	21
Inferior frontal gyrus, pars opercularis L	5	3.39	-60	8	20	-60	9	18
Precentral gyrus L	4	3.72	-60	4	32	-59	5	29
Precentral gyrus L	7	3.63	-48	-12	56	-48	-9	52
Sulcus orbitalis region R	10	3.40	48	28	-8	48	27	-8
Fusiform gyrus R	227	5.42	44	-72	-20	44	-71	-13
Fusiform gyrus L	111	4.89	-44	-72	-24	-44	-71	-17
<i>Monkey</i>								
Inferior parietal lobule R	26	4.02	60	-16	24	59	-14	23
Inferior parietal lobule L	26	4.11	-64	-20	32	-63	-18	30
Inferior parietal lobule/intraparietal sulcus R	75	3.98	36	-52	48	36	-48	47
Inferior parietal lobule/intraparietal sulcus L	87	4.69	-32	-48	40	-32	-45	39
Inferior frontal gyrus, pars opercularis L	16	4.43	-60	8	32	-59	9	29
Superior temporal sulcus R	5	3.86	52	-36	0	51	-35	2
Fusiform gyrus R	207	5.47	44	-72	-16	44	-70	-10
Fusiform gyrus L	158	5.05	-44	-80	-12	-44	-78	-6
<i>Dog</i>								
Inferior parietal lobule L	42	4.59	-60	-32	32	-59	-30	31
Inferior parietal lobule/intraparietal sulcus R	47	3.95	32	-52	44	32	-48	43
Inferior parietal lobule/intraparietal sulcus L	82	3.85	-28	-64	44	-28	-60	44
Inferior frontal gyrus L	9	4.17	-60	4	28	-59	5	26
Middle frontal gyrus R	7	3.28	36	-4	60	36	-1	55
Superior temporal sulcus R	7	3.48	52	-40	4	51	-39	6
Fusiform gyrus R	269	5.83	44	-72	-20	44	-71	-13
Fusiform gyrus L	143	5.37	-44	-72	-24	-44	-71	-17

All *p* values are significant at $p < .001$, after random effect analysis.

R = right; L = left; *k* = number of voxels in cluster; *Z* = peak *Z* value in cluster; *x*, *y*, and *z* = mediolateral, anteroposterior, and dorsoventral spatial coordinates in the MNI average brain and in the TAL space, respectively, both expressed in millimeters.

Table 2. Cortical Cluster Related to the Observation of Oral Communicative Actions

<i>Anatomical Region</i>	<i>k</i>	<i>Z</i>	<i>Spatial Coordinates</i>					
			<i>MNI</i>			<i>TAL</i>		
			<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>
<i>Man (silent speech)</i>								
Inferior frontal gyrus, pars opercularis R	4	3.46	40	12	24	40	13	22
Inferior frontal gyrus, pars opercularis L	117	4.13	-56	24	20	-55	24	17
Inferior frontal gyrus, area orbitalis L	38	3.96	-40	28	-8	-40	27	-8
Superior temporal sulcus L	79	4.27	-56	-36	-8	-55	-35	-5
Superior temporal gyrus R	22	4.25	64	-40	16	63	-38	17
Superior temporal gyrus L	7	3.25	-56	-44	12	-55	-42	13
Fusiform gyrus R	45	4.49	48	-68	-20	48	-67	-13
Fusiform gyrus R	79	4.46	52	-24	-20	51	-24	-16
<i>Monkey (lip-smacking)</i>								
Inferior frontal gyrus, pars opercularis R	21	3.84	56	20	28	55	21	25
Inferior frontal gyrus, pars opercularis L	8	3.62	-52	16	24	-51	17	21
Inferior parietal lobule R	24	3.73	28	-64	60	28	-59	58
Superior temporal sulcus R	7	3.57	52	-36	0	51	-35	2
Fusiform gyrus R	240	5.90	40	-68	-20	40	-67	-13
Fusiform gyrus L	141	5.55	-44	-72	-24	-44	-71	-17
<i>Dog (silent barking)</i>								
Superior temporal sulcus R	24	4.43	52	-36	0	51	-35	2
Fusiform gyrus R	156	5.22	44	-68	-20	44	-67	-13
Fusiform gyrus L	79	4.69	-44	-80	-12	-44	-78	-6

All *p* values are significant at $p < .001$, after random effect analysis.

R = right; L = left; *k* = number of voxels in cluster; *Z* = peak *Z* value in cluster; *x*, *y*, and *z* = mediolateral, anteroposterior, and dorsoventral spatial coordinates in the MNI average brain and in the TAL space, respectively, both expressed in millimeters.

Hence, the stronger activation found during human action observation. Alternatively, it might be that only human actions are represented in the inferior parietal lobule and that the observation of actions made by animals activates these representations thanks to a stimulus generalization.

The second parietal lobe activation was located in the caudal sector of the inferior parietal lobule most likely corresponding to area PG (BA 39). The properties of monkey area PG are less known than those of area PF. It is known, however, that this parietal sector is anatomically linked to the visual occipital areas (see Andersen, Asanuma, Essick, & Siegel, 1990) and has essentially, although not exclusively, visual functions (see Hyvärinen, 1982; for recent data, see Constantinidis & Steimetz, 2001). Previ-

ous brain imaging studies in humans showed that this sector is active during the observation of object related actions, regardless of the effector (hand, mouth, or foot) performing the actions (Buccino et al., 2001). The proposed interpretation of this activation was that area PG is involved in coding object/effector interactions or, alternatively, in signaling an interaction between two objects, even when none of them is a biological effector.

The present data confirm that, regardless of the specific stimulus content, an interaction between an object and a biological effector is a sufficient condition to activate this area. The extent and intensity of PG activation was virtually the same regardless of whether a man, a monkey, or a dog performed the observed action. Because there is no evidence for a mirror activity in this area, the most

parsimonious explanation for this activation is that this area is not part of the mirror neuron system, but plays a role in coding visual stimulus interactions.

It is worth noting that the caudal parietal activation extended into the intraparietal sulcus in that sector where an eye movement representation was described in previous brain imaging studies (Simon et al., 2002; Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Nobre, Gitelman, Dias, & Mesulam, 2000; Corbetta, 1998). We are somehow reluctant to conclude, however, that this activation was exclusively due to saccadic eye movements, because, if this were the case, we should have found it also during the observation of oral communicative actions. It might be, however, that specific pattern of eye movements related to moving objects were responsible for this activation.

The premotor cortex activations during biting observation were located in the pars opercularis of the inferior frontal gyrus (BA 44) and in the adjacent ventral premotor cortex (BA 6). These activations were present on both sides during the observation of biting made by a man, while they were located in the left hemisphere during the observation of biting made by nonconspecifics.

In the monkey, the ventral premotor cortex (area F5 and F4) contains neurons that discharge during actions made with the hand and mouth. Precisely, mouth and distal arm movements are localized in area F5, while reaching movements are represented in area F4 (Gentilucci et al., 1988; Rizzolatti et al., 1988; see Rizzolatti & Luppino, 2001).

Early studies showed that area F5 contains mirror neurons related to hand actions (Gallese et al., 1996; Rizzolatti et al., 1996; Di Pellegrino et al., 1992). More recently, it was found that F5 also contains mirror neurons related to mouth movements. A small part of them are activated by the observation of communicative actions. The large majority discharges during the observation of ingestive actions (Ferrari, Gallese, Rizzolatti, & Fogassi, in press).

Human brain imaging studies showed that a motor representation of hand/arm actions is located in the region straddling the sulcus between the pars opercularis of the inferior frontal gyrus and the ventral area 6 (Ehrsson et al., 2000; Gerardin et al., 2000; Binkofski et al., 1999). Furthermore, recent fMRI and MEG experiments showed that the observation of hand/arm actions activates essentially the same region (Buccino et al., 2001; Nishitani & Hari, 2000; Iacoboni et al., 1999; see also Rizzolatti et al., 2001). The observation of mouth actions activates a region overlapping the one active during the observation of distal arm movements, but more ventrally located with respect to the region related to arm movements (see Buccino et al., 2001). It is important to note that the pars opercularis of the inferior frontal gyrus is considered to be the human homologue of area F5 (Petrides & Pandya, 1997; von Bonin & Bailey, 1947).

The present findings confirm the previous data concerning the observation of biting made by humans and show that the same frontal regions active during the observation of mouth actions made by a man are active also during the observation of actions made by non-conspecifics. As in the case of the rostral parietal activation, an asymmetry was found between the left and right hemispheres. The left activations were virtually identical regardless of the species to which the acting individual belonged, while the right hemisphere activation was absent during the observation of the same action made by a monkey and a dog. It is likely that as for the parietal activation, the left premotor activation was essentially related to the meaning of the action, while the right activation was related also to the pictorial aspects of the stimuli. Note that in the monkey, area PF (the area forming the rostral inferior parietal lobule) and area F5 are tightly linked by reciprocal connections (see Rizzolatti & Luppino, 2001).

Observation of Oral Communicative Actions

The observation of actions with communicative content—silent speech, lip-smacking, and barking—gave a different activation pattern according to the species to which the individual that performed the action belonged.

Speech reading gave a strong activation of the pars opercularis of the left inferior frontal gyrus. An activation of Broca's area during speech reading was not reported in an early study devoted to this topic (Calvert et al., 1997). Note, however, that that experiment was not specifically designed to study frontal activations. All the other experiments on speech reading, including those of the same group of authors, clearly demonstrate that the pars opercularis of the inferior frontal gyrus is active during speech reading (Calvert & Campbell, 2003; Campbell et al., 2001; Surguladze et al., 2001; Grafton, Fadiga, Arbib, & Rizzolatti, 1996). The present data are in accord with these findings.

In the present study, the activation during speech reading (and especially its center of gravity) was located rostral to that found during biting (see Figure 1 and Buccino et al., 2001). The issue of the organization of Broca's area is very complex. There is, however, growing consensus on two points: that different aspects of language processing—semantics, syntax, phonology—have their activation centers in different parts of the left inferior frontal gyrus and that activations of pars opercularis of this gyrus are present also in nonlanguage tasks (see below).

Semantic processing activates predominantly foci in the inferior sector of the region approximately corresponding to its pars orbitalis (see Bookheimer, 2002; Dapretto & Bookheimer, 1999; Fiez, 1997). The localization of syntax processing appears to be more diffuse including sectors of pars triangularis and opercu-

laris. Finally, phonological processing activates a dorso-caudal sector of pars opercularis extending to the adjacent parts of the ventral premotor cortex (see Bookheimer, 2002; Chein, Fissel, Jacobs, & Fiez, 2002). According to some authors, phonology is represented also in a further part of Broca's area, more rostral and ventral than the previous one (Zatorre et al., 1996; see Chein et al., 2002).

The region active during biting observation in the present study was largely overlapping to the posterior phonological sector. It is interesting to note that this sector is also active during the execution of grasping (Ehrsson et al., 2000; Gerardin et al., 2000; Binkofski et al., 1999) as well as during the observation of hand actions (Manthey et al., 2003; Buccino et al., 2001). In addition, some recent data indicate that there are also functional interactions between hand grasping and syllable pronunciation. In a series of psychophysics studies, Gentilucci, Benuzzi, Gangitano, and Grimaldi (2001) asked subjects to grasp objects of different size while pronouncing a syllable printed on the target. Mouth opening and sound production were affected by the grasped object size. More recently, it was also shown (Gentilucci, 2003) that lip aperture and amplitude spectrum of voice was affected by mere observation of hand grasping.

A further focus active during speech reading in the present experiment was localized around the sulcus orbitalis. This region, corresponding to BA 47, becomes active most likely because of subjects' attempts to give meaning to the observed speech (Bookheimer, 2002; Dapretto & Bookheimer, 1999). Note that this focus was not present during the observation of communicative actions made by animals. Finally, activation was present also in the posterior part of the STS bilaterally, as found also by other authors (Calvert & Campbell, 2003; Calvert et al., 1997).

The observation of lip-smacking also gave an activation of the pars opercularis of the inferior frontal gyrus. However, the activation was weaker than that observed during speech reading and showed slight right side prevalence.

The observation of silent barking produced no statistically significant activation in the frontal areas. It may be argued that this lack of activation is due to the fact that in contrast with biting where the action was done on an object, barking is an intransitive (no object related) action. Against this interpretation are the results obtained in a previous experiment in which subjects observed transitive and intransitive actions done by mouth, hand, and foot (Buccino et al., 2001). The premotor areas were activated in both transitive and intransitive action conditions. Congruent with this finding are the recent observations that during the observation of English Sign Language, deaf people showed an activation of the pars opercularis of inferior frontal gyrus (MacSweeney et al., 2002). Thus, the lack of frontal activation during barking observation strongly suggests that silent barking is un-

derstood essentially on visual basis. The fact that visual areas were more active during barking observation than during speech reading reinforces this conclusion.

Final Considerations

Taken together, the results of the present experiment suggest that actions made by other individuals may be recognized in different ways. Actions belonging to the motor repertoire of the observer are mapped on his/her motor system. Actions that do not belong to this repertoire appear to be recognized essentially based on their visual properties.

Biting observation and speech reading both determine resonance of the cortical motor circuits that are involved in their actual execution. For biting, this is true both when the observed action is made by a conspecific and by an individual belonging to a different species. This motor resonance could be interpreted as a translation of an action visually described into an internal "personal" knowledge. The observed action is understood because the motor representation on which is matched produces an outcome that is known to the acting individual.

Actions that are not part of the motor repertoire of the observer and that therefore cannot be reproduced appear to be recognized in nonmotor terms. They are most likely understood based on visual description of the observed events and inferences of their consequences and/or goals. There is clear evidence from monkey experiments (see Jellema & Perrett, 2002; Perrett et al., 1989) and brain imaging studies in humans (for a review, see Allison, Puce, & Mc Carthy, 2000) that a neural system specifically devoted to coding movements made by living beings is located in the STS region. The presence of a strong activation in STS region during barking observation, found in the present study, supports this view.

METHODS

Fourteen healthy, right-handed volunteers (8 men and 6 women; age range: 23–33 years) entered the study. In all of them, right-handedness was established by means of the Edinburgh Inventory (Oldfield, 1971). All subjects had normal or corrected-to-normal visual acuity. They all gave their written informed consent to the experimental procedure, which was preventively approved by the Ethical Committee of the University of Parma.

Experimental Conditions and Stimuli Presentation

The experiment was carried out using a block design. While being scanned, subjects were asked to carefully observe a series of video sequences, each presenting a single mouth action performed by a man, a monkey, and a dog. The mouth actions to observe were (a) biting (Figure 2) and (b) oral communicative actions (Figure 4). The latter were silent speech, silent lip-

smacking, and silent barking made by a man, a monkey, and a dog, respectively. Video sequences were rear-projected onto a screen positioned in front of the scanner. Subjects saw the images through a mirror located inside the scanner.

Each video sequence (experimental block) lasted 20 sec. Over this time, the same action (i.e., biting) was presented four times. As a control, for each video sequence presenting a mouth action, the subjects had to observe a static frame of the same action for 20 sec. Each run consisted of 12 blocks: 6 blocks during which the subjects observed mouth actions, alternated with 6 blocks during which they observed static frames. The different video sequences were pseudorandomly presented within each run. Four runs were performed for each subject.

At the end of the scanning, the subjects were asked to report the actions they saw in the different conditions.

fMRI Data Acquisition

BOLD-sensitive fMRI images were acquired on a General Electric 1.5-T whole-body scanner using standard echo-planar (EPI) sequences and a standard radiofrequency (RF) coil for signal transmission and reception. Thirty consecutive slices oriented parallel to the anterior–posterior commissure plane and covering the whole brain were acquired. The following parameters were used: repetition time: 4 sec; echo time: 60 msec; voxel size: $3.75 \times 3.75 \times 4$; matrix: 64×64 ; field of vision (FOV): 24×24 cm. Structural images were acquired from the same planes using a standard T1 weighted sequence. In addition, high-resolution anatomical images of the whole brain were obtained by using a 3-D fast spoiled gradient-recalled at steady-state sequence with the following parameters: voxel size: $0.97 \times 0.97 \times 1.3$; FOV: 24×24 cm; matrix: $256 \times 256 \times 124$ planes.

Image Analysis

Image analysis was carried out on a personal computer (Pentium IV) using Matlab (Mathworks, Natick, MA) and Statistical Parametric Mapping software SPM99 (Wellcome Department of Cognitive Neurology, London). SPM99 was used for image realignment, image normalization, smoothing (8 mm for group analysis), and to create statistical maps of significant regional BOLD response changes (Friston, 1995, Friston et al., 1995). A kernel filter of $8 \times 8 \times 8$ mm was used. For each single subject, activation maps were first computed by contrasting each active condition with its own control. Subsequently, random effects statistics were calculated for each of the contrasts (Friston, Holmes, & Worsley, 1999). A voxel threshold for statistical significance of $p < .001$ (uncorrected) was adopted for random effects z maps.

The statistical criteria incorporated in the random effects methods and used in this study are intrinsically robust and does not require the use of multiple comparison correction. Furthermore, in the present experiment, the statistical threshold used is further justified by the fact that the main areas of interests in the frontal and parietal lobe were predicted based on a priori hypothesis based on a previous study (see Buccino et al., 2001).

In addition, to compare directly and quantitatively active conditions (after baseline subtraction) in the frontal lobe, where different activations were found during the observation of communicative actions done by individual of different species, we analyzed the time series of the BOLD signal in the left BA 44 (the area involved in the activation) using the general linear model. BA 44 was defined using the cytoarchitectonically maps of Amunts et al. (1999) and the related parameters (Amunts et al., personal communication; www.fz-juelich.de). A voxel was considered part of our region of interest (ROI) when at least 3 out of 10 brain studied by Amunts had that voxel inside area 44. The parameters of this reference brain were transformed to match the MNI reference brain by applying a zoom of 1.16 (x), 1.07 (y), and 1.06 (z). Using MarsBar (Brett, Johnsrude, & Owen, 2002, see also www.mrc-cbu.cam.ac.uk), we then extracted the mean BOLD signal in this ROI for each subject separately, using the spatially smoothed and normalized functional images used for the general SPM analysis. We then modeled the high-pass filtered (120 sec) and smoothed (HRF) time series using the same basis functions used for the general voxel-wise analysis in SPM. The contrast values for (human–static)–(monkey–static), (human–static)–(dog–static), (monkey–static)–(dog–static) were then calculated for each subject. A second-level analysis was then performed, testing the hypothesis that the means of the 14 single subject contrasts were equal to zero using single sample Student's t statistics. This analysis is equivalent to a random effect analysis, but performed on the mean activity in the ROI.

Localization of Activation

The stereotactic coordinates of the pixels of the local maximum significant activation were determined within areas of significant relative activity change associated with the task. The anatomical localization of these local maxima was assessed with reference to the MNI space and then transformed to fit TAL space (www.mrc-cbu.cam.ac.uk). The coordinates of the activations in the pars opercularis of the inferior frontal gyrus were compared with the cytoarchitectonically defined probability map for Broca's area by Amunts et al. (1999 and personal communication). The localization in the pars opercularis was accepted only when it met the criteria established in that article.

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The data reported in this experiment have been deposited in the fMRI Data Center (<http://www.fMRIDc.org>). The accession number is 2-2003-11437.

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