

Language in shadow

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The recent finding that Broca's area, the motor center for speech, is activated during action observation lends support to the idea that human language may have evolved from neural substrates already involved in gesture recognition. Although fascinating, this hypothesis can be questioned because while observing actions of others we may evoke some internal, verbal description of the observed scene. Here we present fMRI evidence that the involvement of Broca's area during action observation is genuine. Observation of meaningful hand shadows resembling moving animals induces a bilateral activation of frontal language areas. This activation survives the subtraction of activation by semantically equivalent stimuli, as well as by meaningless hand movements. Our results demonstrate that Broca's area plays a role in interpreting actions of others. It might act as a motor-assembly system, which links and interprets motor sequences for both speech and hand gestures.

INTRODUCTION

Several theories have been proposed to explain the origins of human language. They can be grouped into two main categories. According to "classical" theories, language is a peculiarly human ability based on a neural substrate newly developed for the purpose (Chomsky, 1966; Pinker, 1994). Theories of the second "evolutionary" category consider human language as the evolutionary refinement of an implicit communication system, already present in lower

primates, based on a set of hand/mouth goal-directed action representations (Armstrong, Stokoe, & Wilcox, 1995; Corballis, 2002; Rizzolatti & Arbib, 1998). The classical view is supported by the existence in humans of a cortical network of areas that become active during verbal communication. This network includes the temporal-parietal junction (Wernicke's area), commonly thought to be involved in sensory processing of speech, and the inferior frontal gyrus (Broca's area) classically considered to be the speech motor center.

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However, the existence of areas exclusively devoted to language has increasingly been challenged by experimental evidence showing that Broca's area and its homologue in the right hemisphere also become active during the observation of hand/mouth actions performed by other individuals (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006; Decety et al., 1997; Decety & Chaminade, 2003; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes, Costes, & Decety, 1998; Grèzes, Armony, Rowe, & Passingham, 2003; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Rizzolatti et al., 1996). This finding seems to favor the evolutionary hypothesis, supporting the idea that the linguistic processing that characterizes Broca's area may be closely related to gesture processing. Moreover, comparative cytoarchitectonic studies have shown a similarity between human Broca's area and monkey area F5 (Matelli, Luppino, & Rizzolatti, 1985; Petrides, 2006; Petrides & Pandya, 1997; von Bonin & Bailey, 1947), a premotor cortical region that contains neurons discharging both when the monkey acts on objects and when it sees similar actions being made by other individuals (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). These neurons, called "mirror neurons," may allow the understanding of actions made by others and might provide a neural substrate for an implicit communication system in animals. It has been proposed that this primitive "gestural" communication may be at the root of the evolution of human language (Rizzolatti & Arbib, 1998). Although fascinating, this theoretical framework can be challenged by invoking an alternative interpretation, more conservative and fitting with classical theories of the origin of language. According to this view, humans are automatically compelled to covertly verbalize what they observe. The involvement of Broca's area during action observation may therefore reflect inner, sub-vocal speech generation (Grèzes & Decety, 2001). Clearly, an experiment determining which of these two interpretations is correct, could provide a fundamental insight into the origins of language.

We investigated here the possibility that Broca's area and its homologue in the right hemisphere become specifically active during the observation of a particular category of hand gestures: hand shadows representing animals opening their mouths. These stimuli have been

selected for two main reasons. First, by using these stimuli it was possible to design an fMRI experiment in which any activation due to covert verbalization could be removed by subtraction: the activation evoked while observing videos representing stimuli belonging to the same semantic set (i.e., real animals opening their mouths), and expected to elicit similar covert verbalization, could be subtracted from activity elicited by hand shadows of animals opening their mouths. Residual activation in Broca's area after this critical subtraction would demonstrate the involvement of "speech-related" frontal areas in processing meaningful hand gestures. Second, hand shadows only implicitly "contain" the hand creating them. Thus they are interesting stimuli that might be used to answer the question of how detailed a hand gesture must be in order to activate the mirror-neuron system. The results we present here support the idea that Broca's area is specifically involved during meaningful action observation and that this activation is independent of any internal verbal description of the seen scene. Moreover, they demonstrate that the mirror-neuron system becomes active even if the pictorial details of the moving hand are not explicitly visible. In the case of our stimuli, the brain "sees" the performing hand also behind the appearance.

METHODS

Participants were 10 healthy volunteers (6 females and 4 males; age range 19–32, mean 23). All had normal or corrected vision, no past neurological or psychiatric history and no structural brain abnormality. Informed consent was obtained according to procedures approved by the Royal Holloway Ethics Committee. Throughout the experiment, subjects performed the same task, which was to carefully observe the stimuli, which were back projected onto a screen visible through a mirror mounted on the MRI head coil (visual angle, $15^{\circ} \times 20^{\circ}$ approximately). Stimuli were of six types: (1) movies of actual human hands performing meaningless movements; (2) movies of the shadows of human hands representing animals opening their mouths; (3) movies of real animals opening their mouths, plus, as controls, three further movies representing a sequence of still images taken from the previously described three videos. Hand movements were performed by a professional shadow artist. All

stimuli were enclosed in a rectangular frame (Figure 1 and online supplementary materials), in a 640×480 pixel array and were shown in grey scale. Each movie lasted 15 seconds, and contained a sequence of 7 different moving/static stimuli (e.g., dog, cow, pig, bird, etc., all opening their mouths). The experiment was conducted as a series of scanning sessions, each lasting 4 minutes. Each session contained eight blocks. In each session two different movie types were presented in an alternated order (see Figure 1, bottom). Each subject completed six sessions. The order of sessions was varied randomly across subjects. The six sessions contrasted the following pairs of movie types: (1) C1 = moving animal hand shadows, C2 = static animal hand shadows; (2) C1 = moving real hands, C2 = static real hands; (3) C1 = moving real animals, C2 = static real animals; (4) C1 = moving animal hand shadows, C2 = moving real animals; (5) C1 = moving animal hand shadows, C2 = moving real hands; (6) C1 = moving real hands, C2 = moving real animals. Whole-brain fMRI data were acquired on a 3T scanner (Siemens Trio) equipped with an RF volume headcoil. Functional images were obtained with a gradient echo-planar T2* sequence using blood oxygenation level-dependent (BOLD) contrast, each comprising a full-brain volume of 48 contiguous axial slices (3 mm thickness, 3×3 mm in-plane voxel size). Volumes were acquired continuously with a repetition time (TR) of 3 seconds. A total of 80 scans were acquired for each participant in a single session (4 minutes), with the first 2 volumes subsequently discarded to allow for T1 equilibration effects. Functional MRI data were analyzed using statistical parametric mapping software (SPM2, Wellcome Department of Cognitive Neurology, London). Individual scans were realigned, spatially normalized and transformed into a standard stereotaxic space, and spatially smoothed by a 6 mm FWHM Gaussian kernel, using standard SPM methods. A high-pass temporal filter (cut-off 120 seconds) was applied to the time series. Considering the relatively low number of participants, a high-threshold, corrected, fixed effects analysis, was first performed by each experimental condition. Pixels were identified as significantly activated if $p < .001$ (FDR corrected for multiple comparisons) and the cluster size exceeded 20 voxels. The activated voxels surviving this procedure were superimposed on the standard SPM2 inflated brain (Figure 1). Clusters of activation were anatomically characterized according to their centers of

mass activity with the aid of Talairach co-ordinates (Talairach & Tournoux, 1988), of the Muenster T2T converter (<http://neurologie.uni-muenster.de/T2T/t2tconv/conv3d.html>) and by taking into account the prominent sulcal landmarks. Furthermore, as far as Broca's region is concerned, a hypothesis-driven analysis was performed for sessions (3)–(6). In this analysis, a more restrictive statistical criterion was used (group analysis on individual subjects analysis, small volume correction approach, cluster size >20 voxels). Only significant voxels ($p < .005$) within the most permissive border of cytoarchitectonically defined probability maps (Amunts, Schleicher, Burgel, Mohlberg, Uylings, & Zilles, 1999) were considered. This last analysis was performed with the aid of the Anatomy SPM toolbox (Eickhoff et al., 2005). Subjects' lips were video-monitored during the whole scanning procedure. No speech-related muscle activity was detectable during video presentation. The absence of speech-related motor activity during video presentation was assessed in a pilot experiment, on a set of different subjects, looking at the same videos presented in the scanner while electromyography of tongue muscles was recorded according to the technique used by Fadiga, Craighero, Buccino, and Rizzolatti (2002).

RESULTS

During the fMRI scanning volunteers observed videos representing: (1) the shadows of human hands depicting animals opening and closing their mouths; (2) human hands executing sequences of meaningless finger movements; or (3) real animals opening their mouths. Brain activations were compared between pairs of conditions in a block design. In addition (4, 5, 6), each condition was contrasted with a "static" condition, in which the same stimuli presented in the movie were shown as static pictures (e.g., stills of animals presented for the same time as the corresponding videos). The comparison between the first three "moving" conditions with each corresponding "static" one, controls for nonspecific activations and emphasizes the action component of the gesture. Figure 1 shows, superimposed, the results of the moving vs. static contrasts for animal hand shadows and real animals conditions (red and green spots, respectively). In addition to largely overlapping occipito-parietal activations, a specific differential activation emerged in the anterior

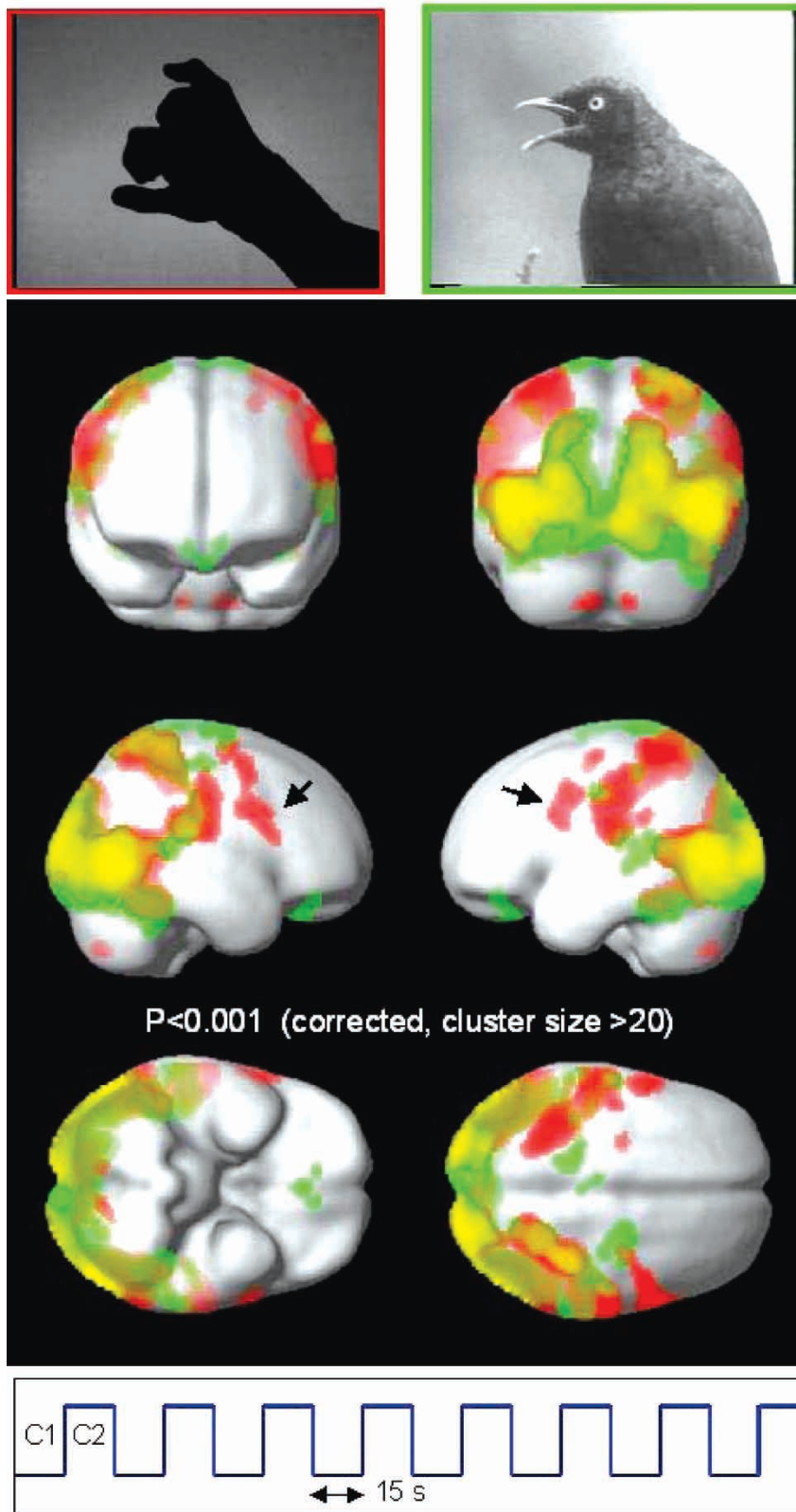


Figure 1 (See opposite for caption)

part of the brain. Animal hand shadows strongly activated left parietal cortex, pre- and post-central gyri (bilaterally), and, more interestingly for the purpose of the present study, bilateral inferior frontal gyrus (BA 44 and 45). Conversely, the only frontal activation reaching significance in the moving vs. static contrast for real animals was located in bilateral BA 6, close to the premotor activation shown in an fMRI experiment by Buccino et al. (2004) when subjects observed mouth actions performed by monkeys and dogs. This location may therefore correspond to a premotor region where a species-independent mirror-neuron system for mouth actions is present in humans. A discussion of non-frontal activations is beyond the scope of the present paper, however the above threshold activation foci are listed in Table 1. The results shown in Figure 1 on one side seem to rule out the possibility that the inferior frontal activity induced by action viewing is due to covert speech, on the other side indicate that the shadows of animals opening their mouths, although clearly depicting animals and not hands, convey implicit information about the human being moving her hand in creating them. Indeed, they evoke an activation pattern superimposable on that evoked by hand action observation (Buccino et al., 2001; Grafton et al., 1996; Grèzes et al., 2003; see Figure 1 and Table 1). To interpret this result, it may be important to stress the peculiar nature of hand shadows: although they are created by moving hands, the professionalism of the artist creating them is such that the hand is never obvious. Nevertheless, the mirror-neuron system is activated. The possibility we favor is that the brain “sees” the hand behind the shadow. This possibility is supported by recent data demonstrating that monkey mirror neurons become active even if the final part of the grasping movement is performed behind a screen (Umiltà et al., 2001). Consequently, the human mirror system (or at least part of it) seems to act more as an active interpreter than as a passive perceiver.

The bilateral activation of inferior frontal gyrus shown in Figure 1 during observation of animal hand shadows cannot yet be attributed to

covert verbalization. This is because it survives the subtraction of still images representing the same stimuli presented in the moving condition, which might also evoke internal naming. It could be argued, however, that videos of moving animals and animal shadows are dynamic and richer in details than their static controls, and might more powerfully evoke a semantic representation of the observed scene, but this cannot be stated with confidence. We therefore made a direct comparison between moving animal hand shadows and moving real animals. We narrowed the region of interest from the whole brain (as in Figure 1) to bilateral BA 44, the main target of our study. This hypothesis-driven analysis was performed by looking at voxels within the most permissive borders of the probabilistic map of this area provided by Amunts et al. (1999) by taking as significance threshold the p value of .005 (random effect analysis). The results of this comparison are shown in Figure 2B. As already suggested by Figure 1 and Table 1, right and (more interestingly) left frontal clusters survived this subtraction. The first one was located in right BA 44 ($X = 58, Y = 12, Z = 24$), an area known to be involved during observation of biological action, either meaningful or meaningless (Grèzes et al., 1998; Iacoboni et al., 1999). The second one is symmetrically positioned on the left side ($X = -50, Y = 4, Z = 22$). Finally, two additional clusters were present in Broca’s region. One was more posterior, in that part of the inferior frontal gyrus classically considered as speech related ($X = -58, Y = 12, Z = 14$; *pars opercularis*) and one more anterior, within area 45 according to the Talairach and Tournoux atlas (1988), ($X = -45, Y = 32, Z = 14$; *pars triangularis*). This finding agrees with our hypothesis and demonstrates that the activation of Broca’s area during action understanding is independent of internal verbalization: if an individual is compelled to verbalize internally when a hand-shadow representing an animal is presented, the same individual should also verbalize during the observation of real animals.

The finding that Broca’s area involvement during observation of hand shadows is not

Figure 1 (opposite). Cortical activation pattern during observation of animal hand shadows and real animals. Significantly activated voxels ($p < .001$, fixed effects analysis) in the moving animal shadows and moving real animals conditions after subtraction of the static controls. Activity related to animal shadows (red clusters) is superimposed on that from real animals (green clusters). Those brain regions activated during both tasks are depicted in yellow. In the lowermost part of the figure the experimental time-course for each contrast is shown (i.e., C1, moving; C2, static). Note the almost complete absence of frontal activation for real animals in comparison to animal shadows, which bilaterally activate the inferior frontal gyrus (arrows).

TABLE 1

Montreal Neurological Institute (MNI) and Talairach (TAL) co-ordinates and *T*-values of the foci activated during observation of moving animal hand shadows, real hands, and real animals, after subtraction of static conditions

	<i>MNI</i>			<i>TAL</i>			<i>T-value</i>
	<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>	
<i>Animal hand shadows</i>							
Inferior frontal gyrus							
BA 44							
R	62	8	24	61	9	22	4.71
L	-62	8	24	-61	9	22	4.58
BA 45							
R	58	22	14	57	22	12	3.37
Precentral gyrus							
BA 6							
R	54	0	36	53	2	33	5.29
	60	2	34	59	4	31	4.90
L	-60	-2	36	-59	0	33	5.09
	-60	0	18	-59	1	17	3.56
	-60	-12	38	-59	-10	36	5.24
BA 4							
R	54	-18	36	53	-16	34	7.97
Postcentral gyrus							
BA 40							
L	-58	-22	16	-57	-21	16	5.92
BA 3							
L	-32	-38	52	-32	-34	50	6.53
BA 2							
R	32	-40	66	32	-36	63	5.18
Superior parietal lobule							
BA 7							
R	26	-48	64	26	-44	61	6.24
Cuneus							
BA 18							
R	16	-100	6	16	-97	10	10.43
	20	-96	8	20	-93	12	12.36
L	-16	-104	2	-16	-101	7	5.09
Middle occipital gyrus							
BA 18							
R	42	-90	8	42	-87	12	7.78
L	-28	-96	2	-28	-93	6	6.95
BA 19							
L	-40	-86	0	-40	-83	4	7.28
Insula							
BA 13							
R	54	-40	20	54	-38	20	6.35
Middle temporal gyrus							
BA 37							
R	54	-70	2	53	-68	5	10.95
Temporal fusiform gyrus							
BA 37							
R	42	-44	-16	42	-43	-11	7.52
L	-44	-44	-16	-44	-43	-11	6.44
Cerebellum							
R	10	-80	-44	8	-80	-42	6.53
L	-8	-78	-44	-8	-77	-33	5.61
Amygdala							
R	22	-2	-22	22	-3	-18	3.85
L	-18	-2	-22	-18	-3	-18	4.15

TABLE 1 (Continued)

	<i>MNI</i>			<i>TAL</i>			<i>T-value</i>
	<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>	
<i>Real hands</i>							
Inferior frontal gyrus							
BA 44							
R	62	16	28	61	17	25	5.67
L	-60	10	26	-60	12	23	3.64
Middle frontal gyrus							
BA 6							
R	34	-6	62	34	-3	57	5.30
L	-24	-8	52	-24	-5	48	4.18
Superior frontal gyrus							
BA 10							
R	4	58	28	4	58	23	6.22
L	-26	54	-2	-27	52	-4	4.14
Postcentral gyrus							
BA 3							
R	52	-20	40	51	-18	38	4.71
BA 7							
R	28	-50	66	28	-46	63	12.50
BA 40							
R	46	-32	54	46	-29	51	4.58
L	-66	-22	14	-65	-21	14	3.37
Inferior parietal lobule							
BA 40							
R	62	-30	28	61	-28	27	4.02
	32	-42	58	32	-38	55	8.23
L	-50	-30	32	-50	-28	31	5.09
	-34	-42	58	-34	-38	55	6.51
Superior parietal lobule							
BA 7							
L	-32	-56	62	-33	-51	60	4.94
Cuneus							
BA 18							
L	-20	-94	6	-20	-91	10	7.13
Middle occipital gyrus							
BA 19							
L	-54	-76	2	-53	-74	6	7.42
	-36	-62	14	-36	-59	16	7.60
Lingual gyrus							
BA 17							
R	10	-96	-8	10	-93	-2	5.74
Inferior occipital gyrus							
BA 18							
R	30	-94	-12	30	-92	-6	6.10
L	-26	-96	-8	-26	-93	-2	6.69
Middle temporal gyrus							
BA 37							
R	52	-68	2	51	-66	5	7.78
Temporal fusiform gyrus							
BA 37							
R	46	-42	-18	46	-41	-13	5.45
L	-46	-44	-16	-46	-43	-11	4.59
Cerebellum							
R	20	-82	-28	20	-81	-20	4.11
L	-28	-56	-50	-28	-56	-39	5.10
Parahippocampal gyrus							
BA 34							
R	30	6	-18	30	5	-15	6.75
Insula							
R	52	-22	18	51	-20	18	6.05

TABLE 1 (Continued)

	<i>MNI</i>			<i>TAL</i>			<i>T-value</i>
	<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>	
Globus pallidus							
R	16	2	2	16	2	2	4.10
L	-16	0	-2	-16	0	-2	3.59
<i>Real animals</i>							
Precentral gyrus							
BA 4							
L	-62	-14	38	-61	-12	36	6.61
BA 6							
R	36	-2	34	36	0	31	5.93
	32	-12	52	32	-9	48	4.48
L	-30	0	38	-30	2	35	10.43
Middle frontal gyrus							
BA 47							
L	-46	48	-2	-46	46	-4	3.92
Superior frontal gyrus							
BA 6							
R	30	-8	72	30	-4	67	3.66
BA 8							
R	20	30	56	20	32	50	6.13
Postcentral gyrus							
BA 2							
L	-38	-40	70	-38	-36	66	4.56
BA 3							
R	34	-36	54	34	-32	51	3.26
L	-18	-44	76	-18	-39	72	3.35
Precuneus							
BA 7							
L	-8	-54	46	-8	-50	45	6.08
Middle occipital gyrus							
BA 18							
R	20	-98	14	20	-94	18	11.75
L	-20	-94	10	-20	-91	14	14.91
BA 19							
R	38	-80	2	38	-77	6	7.21
L	-40	-86	-2	-40	-83	2	9.88
	-54	-76	2	-53	-74	6	8.43
Lingual gyrus							
BA 18							
R	14	-86	-14	14	-84	-8	5.40
L	-6	-88	-10	-6	-86	-4	5.24
Limbic lobe-uncus							
BA 28							
L	-28	8	-24	-28	7	-21	7.00
Superior temporal gyrus							
BA 41							
L	-46	-40	12	-46	-38	13	3.77
Middle temporal gyrus							
BA 21							
L	-54	-24	-8	-53	-24	-6	3.54
BA 37							
R	52	-70	4	51	-68	7	8.03
Temporal fusiform gyrus							
BA 37							
R	44	-42	-20	44	-41	-15	6.50
L	-46	-50	-20	-46	-49	-14	4.66
Cerebellum							
R	46	-58	-32	46	-58	-24	3.55
L	-48	-58	-32	-48	-58	-24	3.78

TABLE 1 (Continued)

	MNI			TAL			T-value
	x	y	z	x	y	z	
Amygdala							
L	-34	-6	-16	-34	-6	-13	3.70
Globus Pallidus							
L	-24	-10	-4	-24	-10	-3	4.93
Anterior Cingulate							
BA 24							
L	-4	36	8	-4	35	6	4.70

Note: BA = Brodmann area; R = right hemisphere; L = left hemisphere; x, y, z = co-ordinates.

explainable in terms of internal speech suggests that, in agreement with other data in the literature, this area may play a crucial role in action understanding. However, it remains the fact that Broca's area is known as a speech area and its involvement during overt and covert speech production has clearly been demonstrated recently (Palmer, Rosen, Ojemann, Buckner, Kelley, & Petersen, 2001). The hypothesis we favor is that this area participates in verbal communication because it represents the product of the evolutionary development of a precursor already present in monkeys: the mirror neurons area F5, that portion of the ventral premotor cortex where hand/mouth actions are represented (see Petrides, 2006). Accordingly, in agreement with the characteristics of area F5 neurons, Broca's area should respond much better to goal-directed action than to simple, meaningless movements. To test this possibility, we performed two further comparisons: (1) The observation of human hands performing meaningless finger movements versus the observation of moving real animals opening their mouths, to determine how much of the *pars opercularis* activation was due to the observation of meaningless hand movements; (2) The observation of animal hand shadows versus the observation of meaningless finger movements, to pit the presence of hands against the presence of meaning. The results are shown in Figure 2, C and D, respectively. After comparison (1), although the more dorsal, bilateral, BA 44 activation was still present (Figure 2C, left: $X = -56$, $Y = 10$, $Z = 26$; right: $X = 58$, $Y = 10$, $Z = 24$), no voxels above significance were located in the *pars opercularis* of Broca's area. This demonstrates that finger movements per se do not activate specifically that part of Broca's area. In contrast, after comparison (2) a significant activation was present in the left *pars opercularis* (Figure 2D;

$X = -58$, $Y = 6$, $Z = 4$), demonstrating the involvement of Broca's area *pars opercularis* in processing actions of others, particularly when meaningful and thus, implicitly, communicative.

DISCUSSION

The finding that animal hand shadows but not real animals or meaningless finger movements activate that part of Broca's region most intimately involved in verbal communication support a similarity between these stimuli and spoken words. Animal hand shadows are formed by meaningless finger movements combined to evoke a meaning in the observer through the shape appearing on a screen. Thus, when one looks at them, the representation of an animal opening its mouth is evoked. Words that form sentences are formed by individually meaningless movements (phonoarticulatory acts), which appropriately combined and segmented convey meanings and representations. Does this twofold involvement of Broca's area reflect a specific role played by it in decoding actions and particularly communicative ones? A positive answer to this question arises, in our view, from the finding that when observation of meaningless finger movements is subtracted from observation of animal hand-shadows, an activation of the left *pars opercularis* persists.

The activation of Broca's area during gestural communication has already been shown in deaf signers, both during production and perception. This was interpreted as a vicariant involvement of Broca's area because of its verbal specialization (Horwitz et al., 2003). In other terms, according to this interpretation, Broca's area is activated because, by signing, deaf people express linguistic concepts. In our study

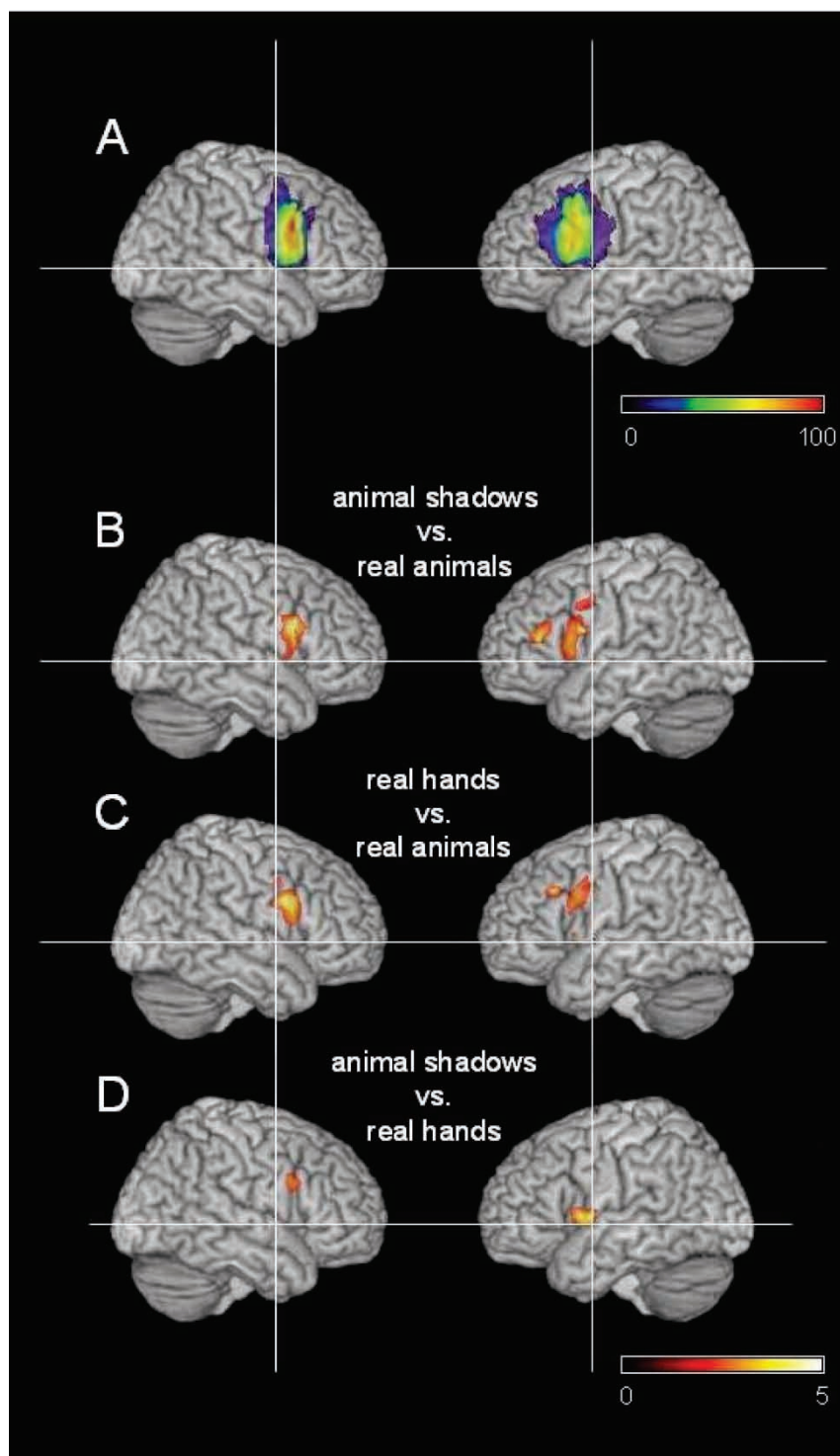


Figure 2 (See opposite for caption)

participants were presented with communicative hand gestures but, in contrast to studies investigating deaf people, the gestures were non-symbolic even if able to address in an unambiguous way a specific concept (e.g., a barking dog). Thus,

we show here, the involvement of Broca's region can not be explained in terms of linguistic decoding of the gesture meaning. Conversely, the results indicate that Broca's region is involved in the understanding of communicative gestures.

How can this “perceptual” function be reconciled with the universally accepted *motor* role of Broca’s area for speech? One possible interpretation is that Broca’s area, due to its premotor origin, is involved in the assembly of meaningless sequence of action units (whether finger or phonoarticulatory movements) into meaningful representations. This elaboration process may proceed in two directions. In production, Broca’s area recruits movement units to generate words/hand actions. In perception, Broca’s area, being the human homologue of monkey area F5, addresses the vocabulary of speech/hand actions, which form the template for action recognition. Our hypothesis is that, in origin, Broca’s area precursor was involved in generating/extracting action meanings by organizing/interpreting motor sequences in terms of goal. Subsequently, this ability might have been generalized during the evolution that gave this area the capability to deal with meanings (and rules), which share similar hierarchical and sequential structures with the motor system (Fadiga, Craighero, & Roy, 2006).

This proposal is in agreement with fMRI investigations that indicate that Broca’s area is not always activated during speech listening. In a recent experiment Wilson, Saygin, Sereno, and Iacoboni (2004) carried out an fMRI study in which subjects (1) passively listened to monosyllables and (2) produced the same speech sounds. Results showed a substantial bilateral overlap between regions activated during the two conditions, mainly in the superior part of ventral premotor cortex. Conversely, the activation of Broca’s region was present only in some of the studied subjects, in our view because the task did not require any meaning extraction. This interpretation is in line with brain imaging studies indicating that, in speech comprehension, Broca’s area is mainly activated during processing of syntactic aspects (Bookheimer, 2002). Luria (1966) had already noticed that Broca’s area patients made comprehension errors in syntactically complex sentences such as passive construc-

tions. Finally, data coming from cortical stimulation of collaborating patients undergoing neurosurgery, showed that the electrical stimulation of the Broca’s area produced comprehension deficits, particularly evident in the case of “complex auditory verbal instructions and visual semantic material” (Schaffler, Luders, Dinner, Lesser, & Chelune, 1993). The data of the present experiment, together with the series of evidence presented above, are in agreement with those theories on the origins of human language that consider it as the evolutionary refinement of an implicit communication system based on hand/mouth goal-directed action representations (Armstrong et al., 1995; Corballis, 2002; Rizzolatti & Arbib, 1998). This possibility finds further support from a recent experiment based on the analysis of brain MRIs of three great ape species (*Pan troglodytes*, *Pan paniscus* and *Gorilla gorilla*) showing that the extension of BA 44 is larger in the left hemisphere than in the right. While a similar asymmetry in humans has been correlated with language dominance (Cantalupo & Hopkins, 2001), this hypothesis does not fit in the case of apes. It might be, however, indicative of an initial specialization of BA 44 for communication. In fact, in captive great apes manual gestures are both referential and intentional, and are preferentially produced by the right hand. Moreover, this right-hand bias is consistently greater when gesturing is accompanied by vocalization (Hopkins & Leavens, 1998).

In conclusion, our results support a common origin for human speech and gestural communication in non-human primates. It has been proposed that the development of human speech is a consequence of the fact that the precursor of Broca’s area was endowed, before the emergence of speech, with a gestural recognition system (Rizzolatti & Arbib, 1998). Here we have taken a step forward, empirically showing for the first time that human Broca’s area is not an exclusive “speech” center but, most probably, a motor assembly center in which communicative

Figure 2 (opposite). Results of the analysis focused on bilateral area 44. (A) Cytoarchitectonically defined probability map of the location of left and right area 44, drawn on the Colin27T1 standard brain on the basis of Juelich-MNI database (Amunts et al., 1999). The white cross superimposed on each brain indicates the origin of the co-ordinates system ($x=y=z=0$). The correspondence between colors and percent probability is given by the upper color bar. (B), (C) and (D), significant voxels ($p < .005$, random effects analysis) falling inside area 44, as defined by the probability map shown in (A), in the three contrasts indicated in the Figure. Color bar: T -values. Note the similar pattern of right hemisphere activation in (B) and (C), the similar location of the posterior-dorsal activation of the left hemisphere in (B) and (C), and the two additional foci in the *pars opercularis* and *pars triangularis* of Broca’s area in (B). Note, in (D), the survival of the activation in *pars opercularis*, after subtraction of real hands from animal hand shadows. When the reverse contrasts were tested (real animals vs. either animal shadows or real hands), the results failed to show any significant activation within area 44.

gestures, whether linguistic or otherwise, are assembled and decoded (Fadiga et al., 2006). It still remains unclear whether hand/speech motor representations are mapped in this area according to a somatotopic organization, or if Broca's area works in a supramodal way, by dealing with effector-independent motor rules.

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