



# Does visual perception of object afford action? Evidence from a neuroimaging study

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## Abstract

Positron emission tomography (PET) was used to explore the neural correlates of a potential involvement of motor representation during the perception of visually presented objects with different tasks. The main result of this study was that the perception of objects, irrespective of the task (judgement of the vertical orientation, motor imagery, and silent generation of the noun or of the corresponding action verb), versus perception of non-objects, was associated with rCBF increases in a common set of cortical regions. The occipito–temporal junction, the inferior parietal lobule, the SMA-proper, the pars triangularis in the inferior frontal gyrus, the dorsal and ventral precentral gyrus were engaged in the left hemisphere. The ipsilateral cerebellum was also involved. These activations are congruent with the idea of an involvement of motor representation already during the perception of object and thus provide neurophysiological evidence that the perception of objects automatically affords actions that can be made toward them. Besides this common set of cortical areas, each task engaged specific regions. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Perception; Object; Action; Intention; PET; Affordance

## 1. Introduction

Knowledge about the use of objects and tools can be based either on the retrieval of instructions of use from semantic memory or on a direct inference of function from structure. The later hypothesis is not far from the notion of affordance, introduced by Gibson [18] and defined as the properties of the animal–environment interactions that determine the consequences of behaviour. According to this theory, the representation of the world rely in part on affordances required for a repertoire of actions. These actions are afforded on the basis of an interaction between the visual attributes of an object and of the goal of the observer. Later Arbib [1] has proposed a model that accounts for perception and action relationships which makes use of the con-

cept of affordance. His thesis is that perception of an object involves gaining access to routines for interaction with the object (motor schemas) but does not necessarily involve execution of even one of these routine.

There are several recent studies in experimental psychology that have explored the existence of an automatic link between the visual perception of an object and a specific predetermined action. For example, Craighero et al. [6] have examined the effects of a prime on a object-determined motor response. They found that a prime visually congruent with an object to be grasped markedly reduces the reaction time for grasping. Such results support the existence of visuo-motor priming. More recently, Tucker and Ellis [57] have performed a series of experiments with a stimulus-response compatibility paradigm using photographs of common graspable objects as stimuli. The aim of their study was to examine the relation between an object's orientation and the hand most suited to perform a reach-and-grasp movement. Objects were presented in two horizontal orientations (one compatible with right-

*Abbreviations:* Ba, Brodmann area; rCBF, regional cerebral blood flow; SPM, statistical parametric map.

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hand grasp, the other with left-hand grasp) and two vertical orientations (upright or reverse). Subjects were requested to decide as fast as possible whether each object was upright or inverted. They reported faster right-hand responses when the object orientation was compatible with a right-hand grasp, and similarly for the left-hand responses. These behavioural results are thus consistent with the view that seen objects automatically potentiate components of the actions they afford, even in absence of explicit intentions to act.

Anatomical and functional distinctions have been made between the dorsal and the ventral streams of visual processing in the brain. The dorsal stream is thought to subservise spatial vision and action, whereas the ventral stream is more implicated in object recognition [59]. However, it is clear that the two systems work in highly integrated fashion [20]. Indeed, actions evoked by familiar objects may be dependent either on the access to semantic knowledge of the object's use, or directly from stored visual knowledge concerning the object [41]. Similarly, it has been hypothesised that both semantic knowledge and sensorimotor experiences may play a role in the recognition of certain objects.

Neuropsychological studies do also support this distinction. For instance, it has been extensively reported that patients with lesions of the ventral stream are impaired in naming and gaining visual access to semantic information about objects, but have preserved ability to make gestures in response to visually presented objects, to recognise and name drawings of actions and pantomimes actions [25,29,30,47,49]. These observations indicate that specific learned gestures or semantic representations are not only activated from vision, but can be evoked directly through the representation of patterns of actions that a particular object specifically affords.

Moreover, Riddoch et al. [42] have reported the case of a patient with 'anarchic hand' behaviour which gives support to Gibson's ecological approach to perception [18]. They used tests in which the patient had to respond to a left-side object with her left hand and to the right-side object with her right hand. Right manual interference effects were found to be influenced by the familiarity of the object; which were explained by the possible left hemisphere dominance for learned responses toward familiar object. Whereas left manual interference responses were elicited by locational and response uncertainty, which may be explained by the fact that the right hemisphere may dominate for the control of the spatial parameters of movements. Their results demonstrate that visual affordances and visual familiarity can directly activate motor responses and thus contribute to action selection. A reverse pattern of results can be observed in patients with parietal lesions that lead to apraxia. While these patients are able to make gestures from object's name, they are impaired at

making actions when objects are visually presented [39]. Further evidence arise from the fact that actions can be affected by the familiarity of the objects. For example, Jeannerod, Decety and Michel [27] have reported the case of a patient with bilateral parietal lesions who showed differences between reaching and grasping familiar and unfamiliar objects. This patient was unable to perform a correct grasp aperture to unfamiliar objects; but with familiar objects, grasp apertures were correctly scaled to the size of the stimuli. This result provides evidence that the semantic information about objects can take part in the control of hand posture.

Therefore, both object recognition and goal-directed behaviour depend on the integrated function of both streams of visual processing. However, it should be emphasised that sensorimotor experience may have a crucial role in processing information to gain access to semantic knowledge only for certain class of objects. The objects recognised should pertain to the category of inanimate and manipulable items, for whose action play a critical part. Indeed, neuropsychological observations have shown such dissociation [48,62]. Moreover, neuroimaging studies [32,38] have demonstrated that the recognition of living and non-living or man-made objects rely on distinct neural substrates. These results suggest that inanimate items are partially identified by their functional significance, while animate items are identified by their physical attributes. For instance, Martin et al. [31] have shown, using PET, that the attributes defining an object are represented close to the cortical region that mediate its perception. These authors suggested that object knowledge may be stored as a distributed network of cortical regions, and the organisation of these regions may be closely parallel the organisation of sensory and motor systems in the human brain.

Finally, within the category of inanimate items, it has also been reported that there is a dissociation between nouns and verbs [8,9,16,40,53], indicating that the information derived from motor channels is likely to be highly salient for the comprehension of actions verbs [62].

It has also been demonstrated that brain regions subserving motor representations, namely the premotor cortex, the ipsilateral cerebellum, as well as the left parietal lobe, are involved during the perception of objects when subjects prepare to act and when they imagine to act upon them (for a recent meta-analysis, see Grèzes and Decety [24]). Moreover, from neurophysiological experiments in monkey, Arbib [2] has argued that the parietal cortex provides affordance information, signalling recognition of situations where a certain motor behaviour is possible.

Thus, there are many behavioural evidence for motor involvement in visual representation of objects [57,6]. The present study was designed to investigate the neu-

ral correlates of the potential implication of motor representations during the perception of manipulable objects. And to assess to what extent would these motor components be involved during the absence of explicit intention to act on the perceived objects. The neural response to the perception of objects was assessed by measuring regional cerebral blood flow (rCBF) with PET in normal subjects while they perceived familiar stimuli with different purposes.

## 2. Materials and methods

### 2.1. Subjects

Ten normal male subjects with a median age of 24 years (range 20–30 years) participated to the study. All subjects were right-handed as tested by Edinburgh Handedness Questionnaire [37]. Subjects gave informed written consent. The study was performed in accordance with the guidelines from the declaration of Helsinki and was approved by the local Ethical committee (Centre Léon Berard). Subjects were paid for their participation.

### 2.2. Experimental design

Subjects lay in a supine position in the PET scanner with their heads immobilised with an individually moulded, rigid thermoplastic face mask that was attached to the scanner's bed to minimise head movements. In addition, control of the head position throughout the examination was made by laser alignment along with reference points on the Reid's line before each session.

PET was used to measure changes in regional cerebral blood flow (rCBF) during the performance of four activation conditions and one baseline condition (Table 1). Stimuli were presented on a mirror suspended 5 cm from the subject's eyes, using a microcomputer-driven video-projector, localised on the back of the scanner.

Color photographs of real graspable objects were used as stimuli. All the objects were capable of being grasped and manipulated by one hand, and were photographed in two horizontal orientations (one compatible with a right-hand grasp, the other with a left-hand grasp) and two vertical orientations (upright and inverted). The objects were photographed so as to appear as if they were resting on a table, at approximately their actual size, at a distance of 50 cm. Examples of stimuli are shown in Fig. 1. Subject's responses were recorded by a computer through its keyboard. Prior to the PET exam, subjects underwent extensive practice with the tasks. Behavioral results comparable to those of Tucker and Ellis [58] for the upright–inverted condition were found.

- For the upright–inverted condition (A), a graspable, familiar tool was presented during 2 s, separated from the earlier by a black screen of 1 s. Subjects were instructed to make a keyboard response, as fast as possible whilst maintaining accuracy, with the left or the right hand depending on whether the objects were upright or inverted. Subjects were told that upside down or upright was defined with regard to the object's normal use. The left–right horizontal orientation of the object was irrelevant to the response. For example in Fig. 1, subjects had to make a right-hand response to the teapot (E) and a left-hand response to the colander (C). This task was performed in order to determine whether objects afford actions even in the absence of explicit intentions to act upon them.
- For the motor imagery condition (I), an object was presented every 3 s. Subjects were instructed to imagine grasping and using each object, then to make a keyboard response with the left or the right hand depending on whether the object was oriented on the left or on the right side. Participants were told that right or left orientation was defined with regard to the object's grasp. For example, as illustrated in Fig. 1, subjects had to make a right-hand response to the coffee-pot, which has its handle oriented on the right side (D), and to make a left-hand response for the teapot (E). Two additional conditions were performed to explore whether action potentiation is independent of the access to stored semantic and verbal knowledge specific to the object presented.
- In the silent object naming task (N), a tool was presented every 3 s. Subjects were instructed to silently name each object, then to make a keyboard response with the left or the right hand depending on whether the object was oriented on the left or on the right side.

Table 1  
Five scanning conditions repeated in each subject

Stimuli	Task instruction	Abbreviation
Non-objects	Judgement of the larger border of the non-object	C
Tools	Judgement of the vertical orientation of the object (upright or reverse)	A
Tools	Mental simulation of grasping and using + judgement of the horizontal orientation (left or right) of the object	I
Tools	Silent tool naming + judgement of the horizontal orientation (left or right) of the object	N
Tools	Silent verb generation + judgement of the horizontal orientation (left or right) of the object	V



Fig. 1

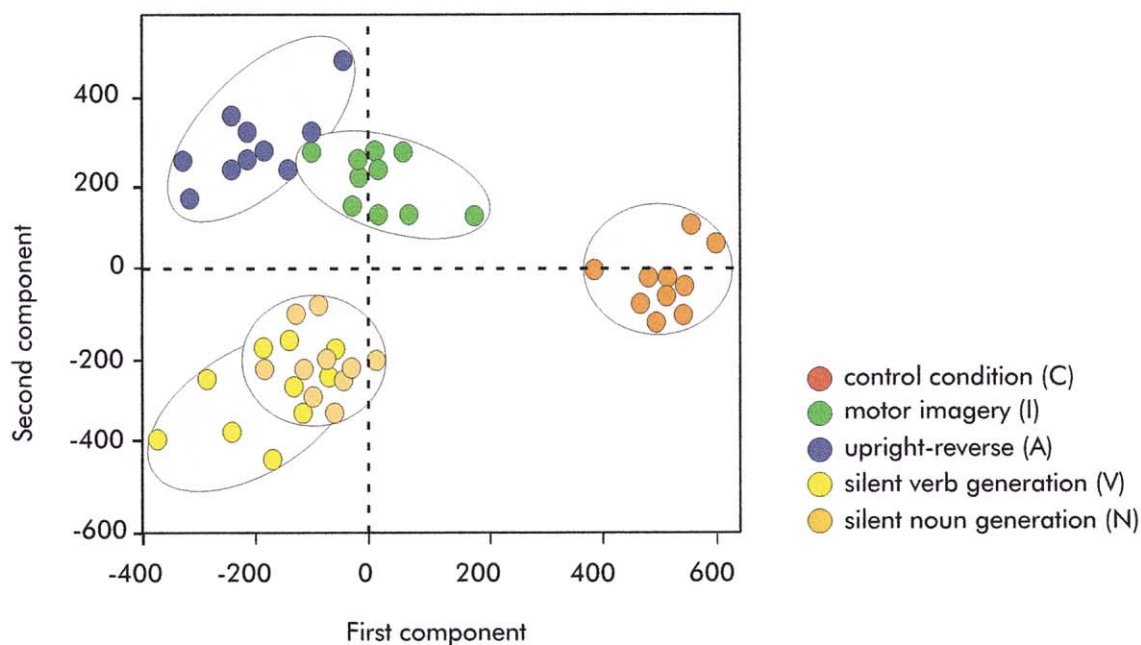


Fig. 2

Fig. 1. Examples of the stimuli used in the experiment. A and B, non-objects presented in the baseline condition (A, left-hand response; B, right-hand response). C–F, objects used in the four activation conditions. (C) left orientation compatible with left-hand grasp, inverted (colander); (D) right orientation compatible with right-hand grasp, upright (coffee-pot); (E) left orientation, upright (teapot); (F) right orientation, inverted (frying pan).

Fig. 2. The first two components of the principal analysis. The first component ( $x$ -axis) clearly separates the baseline condition from the others. Whereas the second one ( $y$ -axis) isolates mental simulation and upright–reverses tasks from the silent generation of nouns and verbs.

- In the silent verb generation condition (V), a tool was presented every 3 s. Subjects were requested to silently say the use of each tool, i.e. access to the action verb, then to make a keyboard response with the left or the right hand depending on whether the object was oriented on the left or on the right side.
- Finally, for the baseline condition (C), a non-object

was visually presented every 3 s. Subjects were instructed to make a keyboard response with the right or the left hand depending on whether the non-object was larger on the right or on the left side. Earlier photographs of tools were manipulated and transformed with Adobe Photoshop™, in order to keep a three-dimensional form, as well as colours and brightness among conditions.

During the PET session, each condition contained 25 trials, and lasted 75 s. Task presentation started 15 s before the radioactive tracer reached the brain. The ratio of right and left hand-responses during the conditions was 80:20 overall, but their distribution was not homogeneous. This was done on purpose. During the period that most strongly determines hemodynamic variation, i.e. the 45 s following arrival of tracer to the brain, trials were right hand-responses. Both the first and the last 15 s of the task, which occurred outside the scanning window, always contained 50% of left hand-responses and 50% of right hand-responses. Subjects were unaware of this manipulation.

The motor imagery, silent verb generation and object naming tasks were equated to the upright–reverse task in terms of hand response ratio in order to lateralise rCBF changes.

Each condition was repeated twice. The order of scan condition was randomised both within and between subjects. Prior to each PET scan, a practice trial composed by five stimuli was administered. The stimuli used in the practice trial were different from those during the scanning period. Objects were different between each condition.

### 2.3. Data acquisition

The PET scans were acquired using a Siemens CTI HR+ (63 slices, 15.2 cm axial field of view) PET tomograph with collimating septa retracted operating in high sensitivity three-dimensional mode. 63 transaxial images with a slice thickness of 2.42 mm without gap in between were acquired simultaneously. Emission scans were attenuation corrected with a transmission scan collected before the experiment during the exposure  $^{68}\text{Ge}$  (9 mCi per pin) external rotating source. After a 9-mCi bolus injection of  $\text{H}_2^{15}\text{O}$ , scanning was started when the brain radioactive count rate reached a threshold value and continued for 45 s. Integrated radioactivity accumulated in 45 s of scanning was used as an index of rCBF. Ten minutes elapsed between each injection.

### 2.4. Data analysis

Image analysis was performed on Silicon Graphics O2 stations. The data were analysed with statistical parametric mapping (SPM96 software Wellcome Department of Cognitive Neurology, UK, Friston et al. [15]) implemented in Matlab 4.2 (Math Works, Natick, MA, USA). The scans of each subject were realigned, with the first scan as reference. The realigned PET images were transformed into a standard stereotaxic space [52] using a reference template image [15]. Images were then smoothed with an isotropic Gaussian filter of 12-mm full-width at half-maximum. The resulting voxel

dimensions of each reconstructed scan was  $2 \times 2 \times 4$  mm in the  $x$ ,  $y$  and  $z$  dimension, respectively. Global differences in cerebral blood flow were covaried out for all voxels and comparisons across conditions were made using  $t$  statistics with appropriate linear contrasts, and then converted to  $Z$  scores. Regional activations significant at  $P < 0.001$  or  $0.0001$  ( $Z > 3.09$  or  $3.72$ , respectively) uncorrected for multiple comparisons were considered. In addition to this standard procedure, and in order to improve the precise anatomical description, the activation foci were superimposed on a reference MRI from one normal subject, available in SPM96. Anatomical identification was performed with reference to the atlas of Talairach and Tournoux [52], as well as the atlas of Duvernoy [12].

#### 2.4.1. Canonical variates analysis

The global condition task effects were assessed using MANOVA and CVA. This approach provides for statistical inference about activation effects and describes important features of these effects. It implicitly takes account of spatial correlation in the data without making any assumptions. This analysis differs fundamentally from statistical parametric mapping, because the statistical inference is about the whole image volume not any component of it. Therefore, this difference ensures that SPM and multivariate approaches are distinct and complementary approaches to functional imaging data [14]. The first step in multivariate analysis was to transform the original data in a set of orthogonal principal components (60 eigenvectors), to ensure that dimensionality (number of components or voxels) of the data is smaller than the number of observations. Only the first six eigenvectors (which represent 80% of the whole variance) were used in the subsequent analysis. The resulting matrix was subject to Mancova, and the significance of the condition effects was assessed with Wilk's Lambda. The threshold for condition effects was set at  $P < 0.001$ . The condition effects accounted for the two first canonical images.

#### 2.4.2. Main effect

A main effect of all target conditions in comparison with the control condition was performed in order to reveal regions common to all four target conditions. The following contrast was performed  $(A + I + N + V) - C$ , masked with each simple contrast  $((A - C), (I - C), (N - C), (V - C))$ . This masking procedure in SPM eliminates voxels that are not significant at  $P < 0.01$  in each specified contrast.

#### 2.4.3. Simple contrasts

The aim of the linear contrasts was to identify regional activation for each target condition relative to the control condition. The following contrasts were performed  $(A - C), (I - C), (N - C), (V - C)$ , where  $A$ ,

upright-inverted judgement; I, motor imagery; N, silent name generation; V, silent verb generation.

### 3. Results

#### 3.1. Subject's performance

During the experiment, the subjects achieved more than 80% correct responses in all conditions (98% in A, 94.4% in I, 94.2% in N, 91.6% in V and 86.4% in C).

#### 3.2. Canonical variates analysis

The first canonical image clearly separates the baseline condition (C) from others; whereas the second canonical image dissociates the upright–reverse task

(A) and the motor imagery task (I) from the silent verb and noun generation tasks (N and V) (see Fig. 2).

#### 3.3. Areas common to the perception of objects

The main effect revealed rCBF increases, located in the SMA-proper, in ventral precentral gyrus, in the inferior frontal gyrus (Ba 45) and in the inferior parietal lobule (Ba 40) in the left hemisphere. Significant activations were also found in the occipito–temporal junction (Ba 19/37), and in the posterior cingulate gyrus in the left hemisphere. The ipsilateral cerebellum and the caudate nucleus were also involved in the right hemisphere (see Fig. 3 and Table 2).

#### 3.4. Specific brain areas engaged by the upright–reverse judgement task

In addition to the common set of cortical areas (see

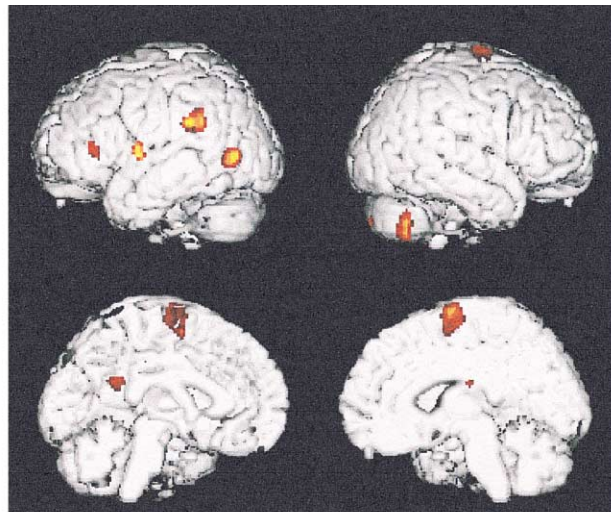


Fig. 3

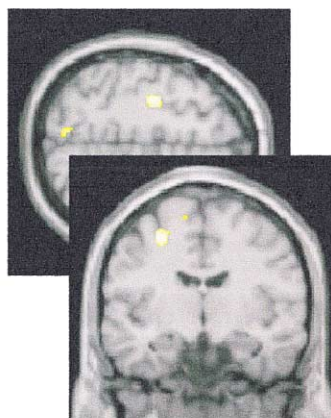


Fig. 4

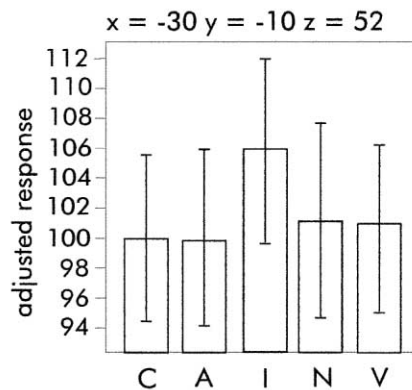


Fig. 3. Areas common to the perception of objects. Localisation of significant rCBF changes rendered onto lateral (top) and medial (bottom) views of the left and the right hemispheres of a standard template irrespective of the subject's intention. Results are listed in Table 2.

Fig. 4. Activated cluster in the premotor cortex during the mental simulation task displayed into coronal and horizontal planes of a standard MRI. Mean adjusted rCBF and standard deviation at the maximum Z-score of this area are illustrated on the right of the figure ( $x = -30$ ,  $y = -10$ ,  $z = 52$ ).

Table 2

Set of cortical brain regions engaged during the perception of objects, irrespective of the task, revealed by a main effect with a threshold of  $P < 0.001$ ,  $Z$  score  $> 3.09$

Brain region	Co-ordinates			Z score
	x	y	z	
<i>Perception of objects, irrespective of the task</i>				
SMA	6	-6	72	4.35
L Inferior parietal lobe	-52	-44	30	4.07
L Posterior cingulate gyrus	-6	-48	24	4.09
R Caudate nucleus	18	-18	22	4.25
L Inferior frontal gyrus (Ba 45)	-40	28	8	3.98
L Ventral opercular precentral gyrus	-58	-2	6	4.32
L Occipito-temporal junction	-50	-68	4	4.87
R Cerebellum	48	-62	-48	4.30

above), this condition yielded activations located in the anterior cingulate gyrus, in the middle and inferior frontal gyri, in the temporo-parietal junction in the right hemisphere. Two rCBF foci were also detected in the right middle temporal gyrus. At the subcortical level, increased activity was found in the right putamen (see Table 3).

### 3.5. Specific brain areas engaged by the motor imagery task

During mental simulation, activations were found in the dorsal precentral gyrus at the level of hand representation, in the middle frontal gyrus, in the posterior part of the superior parietal lobule in the left hemisphere. In the right hemisphere, there were activation foci located in the anterior cingulate gyrus, in the

Table 3

Set of cortical brain regions detected during the perception of tools with the aim to judge their vertical orientation versus the control condition, with a threshold of  $P < 0.001$ ,  $Z$  score  $> 3.09$

Brain region	Co-ordinates			Z score
	x	y	z	
<i>Upright-inverted judgement</i>				
R Anterior cingulate gyrus	12	22	24	4.16
R Middle frontal gyrus	42	44	24	3.56
R Temporo-parietal junction (19/39)	46	-66	16	3.75
R Inferior frontal gyrus	58	24	-4	3.35
R Middle temporal gyrus (Ba 21)	48	-28	-6	3.55
R Putamen	28	-2	-8	3.41
R Middle temporal gyrus (Ba 21)	50	-4	-20	3.83

Table 4

Set of cortical brain regions engaged during motor imagery versus the control condition, with a threshold of  $P < 0.001$ ,  $Z$  score  $> 3.09$

Brain region	Co-ordinates			Z score
	x	y	z	
<i>Motor imagery</i>				
L Precentral gyrus	-30	-10	52	4.55
L Precuneus/LPS	-6	-68	44	3.78
L Middle frontal gyrus	-34	38	34	6.24
R Anterior cingulate gyrus	18	32	28	3.50
R temporo-parietal junction	66	-52	20	3.48
R Inferior frontal gyrus	52	24	-2	3.36
R Putamen	24	-6	-4	3.30

temporo-parietal junction, in the inferior frontal gyrus. At the subcortical level, activations were detected in the right putamen (see Fig. 4 and Table 4).

### 3.6. Specific brain areas engaged by the silent verb generation task

This condition yielded left hemispheric activations located in the pars opercularis (Broca area 44), in the precentral gyrus and in the middle frontal gyrus. Additional rCBF increases were detected in the angular gyrus, in the middle temporal gyrus and in the fusiform gyrus (see Table 5).

### 3.7. Specific brain areas engaged by the silent noun generation task

This condition was associated with left hemispheric activations located in the precentral gyrus, in the middle gyrus, in the pars opercularis (Ba 44). The middle temporal and in the fusiform gyri were also revealed in the left hemisphere (see Table 6).

Table 5

Set of cortical brain regions engaged during silent verb generation versus the control condition, with a threshold of  $P < 0.001$ ,  $Z$  score  $> 3.09$

Brain region	Co-ordinates			Z score
	x	y	z	
<i>Silent verb generation</i>				
L Precentral gyrus	-56	-8	44	3–93
L Angular gyrus	-48	-62	32	4.49
L Middle frontal gyrus	-32	40	32	4.00
L Pars opercularis	-46	16	6	4.92
L Middle temporal gyrus	-62	-42	0	4.58
L Fusiform	-36	-30	-18	4.73

Table 6

Set of cortical brain regions engaged during silent verb generation versus the control condition, with a threshold of  $P < 0.001$ ,  $Z$  score  $> 3.09$

Brain region	Co-ordinates			Z score
	x	y	z	
<i>Silent noun generation</i>				
L Precentral gyrus	−56	−6	44	3.59
L Middle frontal gyrus	−32	38	34	3.88
L Pars opercularis	−48	16	10	5.09
L Middle temporal gyrus	−56	−30	2	3.98
L Fusiform	−36	−30	−16	4.35

### 3.8. Common brain regions between the upright–reverse and the imagery tasks

In both upright–inverted and motor imagery tasks, rCBF increases were detected in the anterior cingulate gyrus, in the temporo–parietal junction, in the inferior frontal gyrus, and in the putamen in the right hemisphere.

### 3.9. Common brain regions between silent verb and noun generation tasks

The silent verb and noun generation tasks shared common activations located in the inferior frontal gyrus (Ba 44), in the precentral, middle frontal, in the middle temporal and in the fusiform gyri in the left hemisphere.

## 4. Discussion

Affordances are preconditions for activity. The presence of a given situation within the environment that provides an affordance for some activity does not imply that the activity will occur, although it contributes to the possibility of that activity [23]. We designed this experiment to explore to what extent action codes are activated automatically by visual stimuli, searching for correlating neural activity in cortical regions known to be involved in action generation, with an event that need not to occur.

### 4.1. Common network

The perception of objects, irrespective of the subject's intention, was associated with a common set of cortical areas that can be interpreted as partial involvement of motor representations. This neural network consists of several foci localised in the inferior parietal lobule, in premotor cortex, in the SMA-proper and in the inferior frontal gyrus (Ba 45) and the ipsilateral cerebellum. An

additional foci was found in the MT/V5 complex. These results fit well with the functional distinction between the two major projections from primary visual cortex. The ventral pathway is associated with object recognition, whereas the dorsal pathway, projecting to the frontal lobe, is involved in the control or representation of object related actions [35].

The activation of the motion-selective area MT/V5 during the perception of static stimuli (photographs of objects) may sound intriguing. Earlier brain imaging studies, using either PET or fMRI, have consistently shown that human cortical areas MT (V5) and MST respond to moving stimuli (e.g. [51,56,63]), stationary stimuli inducing motion [55,64], apparent motion and motion imagery [19,50]. MT/V5 is the first area of the dorsal processing stream, which mediates the visual control of skilled actions, such as manual prehension directed to objects [20]. There are now converging evidence that visual motion is sufficient but not necessary to activate MT/V5 and our result is consistent with this notion. MT/V5 is thus also involved in the construction of representation of gestures triggered by the visually presented object.

The association of parietal and premotor activations is coherent with the model proposed by Arbib [2], which tags the movement representation area as premotor and driven by visual affordances for movements computed in the parietal cortex. This model has been elaborated from electrophysiological recordings in monkey. For instance, Sakata et al. [46] have demonstrated that a neural representation of 3D objects with real physical dimensions and their egocentric positions and movements occur in the parietal association cortex. According to these authors, the major purpose of this coding is the visual guidance of goal-directed action, in which the parietal cortex plays an essential role. Moreover, the brain region in which this kind of neurons have been recorded (i.e. anterior intraparietal AIP) is reciprocally connected to the ventral premotor (F5) area which send signals to the motor cortex. Rizzolatti et al. [44] have discovered, in the ventral premotor (area F5) in monkey, canonical neurons that fire in both in response to 3D object presentation and during execution of a specific action which is compatible to the use of the object. The interpretation given was that there is a close link between common 3D objects and the action necessary to interact with them; and thus each time a graspable object is presented, the related F5 neurons are addressed and the action is 'automatically' evoked [36]. Therefore, F5 neurons would provide a 'vocabulary' of motor elements for constructing possible motor grasps, which operates by matching the affordances of the object as analysed by AIP neurons [17,45]. Recent neuroimaging studies have revealed this part of the inferior parietal region during complex manipulation of objects and lead to suggest that it might correspond to AIP in monkey [4].

The involvement of left inferior parietal lobule is coherent with evidence raised by Castiello et al. [5] that this region codes affordance besides its role in motor planning. There are also several results from neurophysiological studies that have shown that posterior parietal cells synthesise a neuronal representation of intended movements, regardless of whether the movement is executed [7]. Our study provides new evidence, in human, as to the role of the inferior parietal lobule in encoding possible motor behaviour, at the representational level that specify the general class of hand shape required to interact with objects rather than the very precise parameters specification associated with actually executing a movement [58].

The activation found in the premotor cortex in all target conditions (same level of rCBF activity for all target conditions within this voxel), in its opercular part at 6 mm above the AC-PC line, lies in the ventral premotor region (PMv). Interestingly, Fink et al. [13] have reported rCBF augmentations elicited by finger movements at the very same co-ordinates.

There was no activation of Brodmann area 44 in the inferior frontal gyrus but an rCBF increase was detected in the pars triangularis (Ba 45). This activation is more posterior to that found by Grafton et al. [22] during the perception of objects, silent object naming, and silent object-use naming. Rizzolatti et al. [43] as well as Grafton et al. [21] reported a specific increase in the rostral part of Broca's area (i.e. Ba 45) during the observation of grasping movements towards objects. The cytoarchitectonic organisation of F5 is not homogeneous but consists of various sectors [33] and the inhomogeneity indicates that both areas 44 and 45 would originate from an area homologous to F5 [3]. According to these authors, F5 serves two functions — one that mediates visuomotor transformation for selecting hand-grip according to the object's intrinsic properties and a second related to grasping [44].

The lack of involvement of the ventral stream can be related to the suggestion made by Hodges et al. [26] that sensory inputs to a parietal system can trigger the use of object without reference to object-specific conceptual knowledge.

Altogether, the concomitant activation within both parietal and premotor regions during the perception of objects is a strong evidence in favour of the 'automatic activation' of relevant actions that they afford.

#### 4.2. *Mental simulation and upright–reverse tasks*

In addition to the common network, the mental simulation task was associated with several specific activated areas in the precentral gyrus, the superior parietal lobule and the middle frontal gyrus in the

left hemisphere. Neural correlates of mental motor simulation has been extensively investigated using neuroimaging techniques (for a review see Decety [11]). Our results are consistent with what has been earlier found, and give further support to the fact that consciously representing an action involves a pattern of cortical activation that resembles that of an intentionally executed action.

The upright–reverse task engaged common sites of activation with mental simulation task which are right-hemispheric localised, including the temporo–parietal junction, the anterior cingulate and the inferior frontal gyri. Interestingly the area in the temporo–parietal region corresponds to the lesion site in patients, which is often associated with neglect [60]. It was recently proposed that the right inferior parietal lobe is involved in the initial stages of generating motor intention in addition to its important role in visual awareness [34].

#### 4.3. *Silent nouns and verb generation tasks*

The internal retrieval of verbs or nouns in response to objects was associated with activations in Broca area 44 and in the precentral gyrus. There are a number of neuroimaging studies that have already reported such activation during silent generation [22,61]. The left middle temporal gyrus (Ba 21) has been consistently involved across studies for the recognition of action related items. Area 21 was found to be activated in PET studies in which subjects generated action words or named tools [31,32], or during the observation of object related actions [10,43]. According to Martin et al. [31], this region may be a critical site for stored knowledge about the visual patterns of motion associated with the use of objects.

Additional activation localised in the angular gyrus was detected only for the verb generation task. This result is not surprising since there are several clinical and experimental studies, which have shown that nouns and verbs can be independently disrupted by brain damage [15,54]. The activation within the parietal cortex may be related to the division of labour between nouns and verbs in the representation of motion as proposed by Kersten [28]. According to this author, verbs are specialised to convey relational information, whereas nouns convey information about individual objects. This distinction between intrinsic and extrinsic motion may be related to the neuroanatomical distinction between the 'what' and 'where' systems. This idea ties up with Damasio et al. [8] hypothesis that the systems that mediate access to verb are anatomically close to those that support concepts of movement and relationship in space-time.

## 5. Conclusion

The set of cortical regions found to be involved in all target conditions provides strong neurophysiological evidence to the concept of affordance. One question remains, however, as to whether or not the same neural network would be engaged during real ecological conditions, which often correspond to the perception of objects without any specific cognitive task or even intention to act upon them.

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