

Different Brain Correlates for Watching Real and Virtual Hand Actions

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Received November 8, 2000

We investigated whether observation of actions reproduced in three-dimensional virtual reality would engage perceptual and visuomotor brain processes different from those induced by the observation of real hand actions. Participants were asked to passively observe grasping actions of geometrical objects made by a real hand or by hand reconstructions of different quality in 3D virtual reality as well as on a 2D TV screen. We found that only real actions in natural environment activated a visuospatial network including the right posterior parietal cortex. Observation of virtual-reality hand actions engaged prevalent visual perceptual processes within lateral and mesial occipital regions. Thus, only perception of actions in reality maps onto existing action representations, whereas virtual-reality conditions do not access the full motor knowledge available to the central nervous system.

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INTRODUCTION

Virtual-reality (VR) technology is being used as an alternative to reality in a wide spectrum of disciplines, including engineering, electronic videogames, architecture, physics, chemistry, medicine, and the military (Brooks, 1999). VR stimuli are of broad interest because of their possible applications to training of athletes; to rehabilitation of motor, spatial, and cognitive deficits in neurological diseases; and in clinical psychology, to palliate selective symptoms such as pain and fear (Wiederhold and Wiederhold, 1998). Despite the common belief that VR technology can be used as an alternative to reality, no evidence exists of neural equivalence between the perception and the elaboration of VR and real stimuli. This equivalence is assumed, however, in neuroscience, when VR is used to investigate spatial (Aguirre *et al.*, 1996), visuomotor

(Decety *et al.*, 1994; Ghahramani and Wolpert, 1997) and emotional (Nakamura *et al.*, 1999) processing.

In this study, we compared the human brain processes that support the observation of object-grasping actions performed by a real hand with those supporting the observation of the same object-related movements performed by virtual-reality reconstructions of the same human hand. This work, extending our previous limited observations (Decety *et al.*, 1994), provides definitive evidence of the different roles of reality and virtual reality in influencing neural processing during action observation/recognition.

Many researchers argue that recognition of actions of conspecifics is an ability that is highly developed in humans and nonhuman primates (Premack and Woodruff, 1978). Why is an action perceived as such? Some studies have shown that, even when a limited number of kinematic cues are available, such as lights attached at the main joints, humans can easily distinguish biological motion from impulsion produced by mechanical devices (Dittrich, 1993). It has been postulated that, under normal viewing conditions, observed actions can be understood and imitated whenever they become the source of a representation of those actions. Observation of actions is the first step in imitation, a powerful means of establishing contact with other individuals and acquiring new skills from them. Imitation starts at birth and continues throughout life (Meltzoff and Moore, 1977). Observation of hand actions is the fundamental process used by profoundly deaf people in acquiring and using sign language (Hickok *et al.*, 1996). Positron emission tomography (PET) experiments in humans observing motor acts performed by real hands have shown activations of neural networks that are partially overlapping with those operating during motor planning and execution (Grafton *et al.*, 1996; Rizzolatti *et al.*, 1996).

Here we tested the hypotheses that the interaction of the neural systems with 3D virtual space, and/or the degree of realism in the reproduction of virtual-reality items, may induce different patterns of activation relative to the processing of real movements

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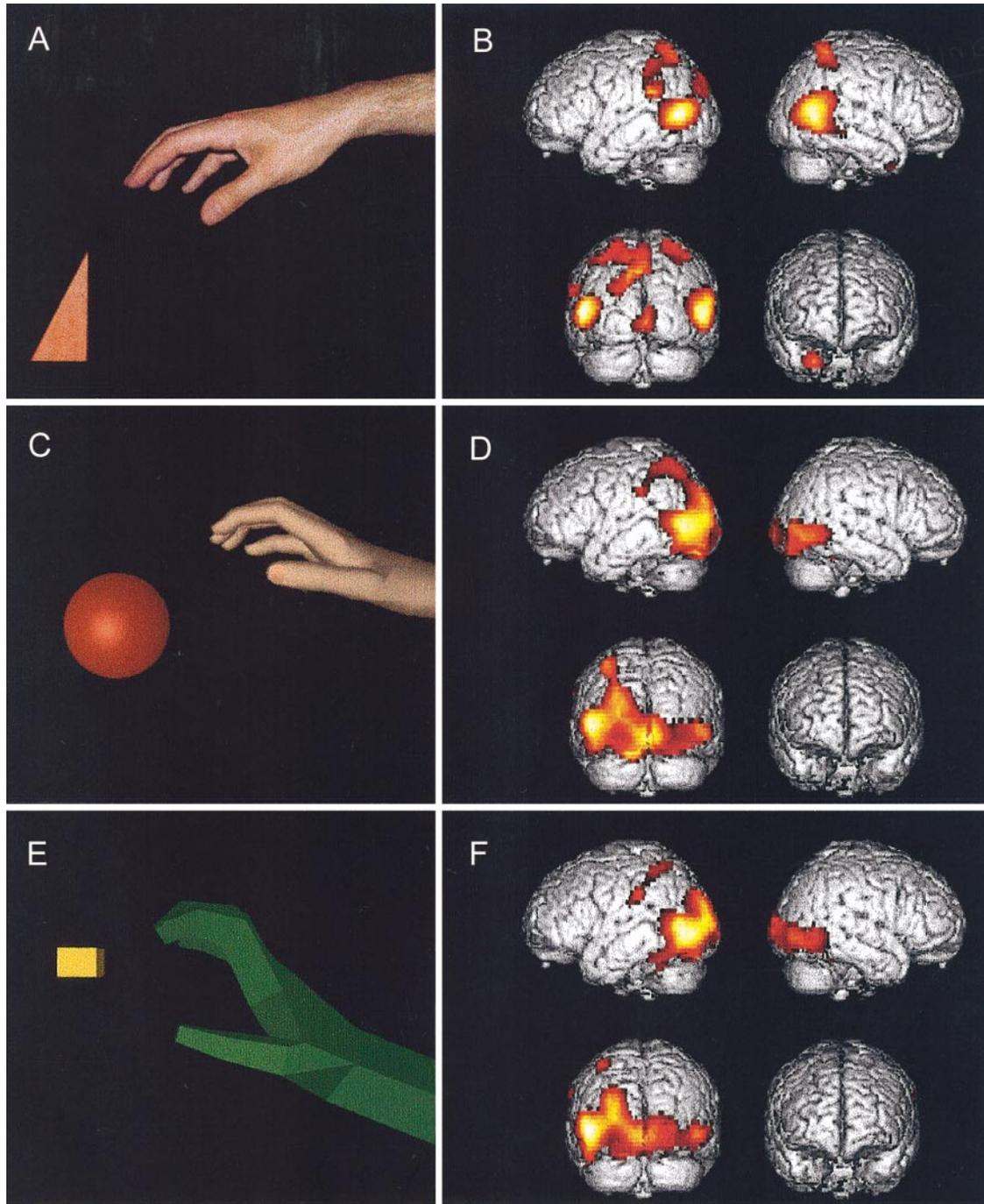


FIG. 1. Simple main effects. On the left, snapshots of the RE, VRH, and VRL hand grasping a geometrical object are displayed for comparison of shape and texture differences (A, C, E). On the right side, the corresponding regions of significant activation for the three experimental conditions in comparison to the baseline (observation of geometrical objects: OGO), superimposed on standard SPM96 cortical three-dimensional renderings (B, D, F). (A and B) RE vs OGO; (C and D) VRH vs OGO; (E and F) VRL vs OGO. Red-yellow scale, significant activation foci; gray scale, cortical 3D reconstruction.

in a real environment. Subjects were studied with PET while they observed object-grasping actions performed by a real right hand (RE) in comparison with the same actions reproduced by means of 3D virtual-reality, either of a high (VRH) or of a low virtual-

reality (VRL) level (see Figs. 1A, 1C, and 1E). In a second PET experiment, normal volunteers observed on a TV screen 2D movie sequences of the same object-related grasping actions performed by a real hand.

METHODS

Subjects

In the first experiment, the participants included eight subjects, with an age range of 24–28 years. In the second experiment, additional data were collected in a separate group of eight subjects (age range 22–26). All subjects were right-handed. None of them had a history of neurologic or psychiatric conditions. The experimental protocols were approved by the local hospital ethics committee.

PET Data Acquisition

We measured rCBF by recording the distribution of radioactivity following an intravenous injection of ^{15}O -labeled water with a 3D GE Advance scanner (General Electric Medical Systems, Milwaukee, WI). Participants received a 5-mCi slow bolus of H_2^{15}O , 4 cc in 20 s, plus 4 cc of saline solution in 20 s (Silbersweig *et al.*, 1993). After attenuation correction, the data were reconstructed as 35 transaxial planes by 3D filtered back projection with a Hanning filter (cut-off 4 mm filter width) in the transaxial plane and a Ramp filter (cut-off 8.5 mm) in the axial direction. The index of rCBF was the integrated counts collected for 90 s, starting 30 s after injection time.

Experimental Set-up

The participants laid in a PET scanner with their heads immobilized. Black curtains were arranged around and in front of the participants, so that they could focus only on what was shown behind a single rectangular opening (40×40 cm) in front of them. This environment provided an immersive condition. For all the tasks of experiments 1 and 2, the participants were instructed to carefully observe what was appearing through the curtain opening and to avoid inner verbalization. They could observe the motion sequences played either in reality (RE condition) or on a computer (VR conditions) or on a TV screen (TV condition).

(1) In the first PET experiment the tasks were as follows:

RE: a real hand grasping real geometrical objects.

VRH: a “realistic” virtual hand grasping virtual geometrical objects.

VRL: a coarse virtual hand, close to a robotic hand, grasping virtual geometrical objects.

Each experimental condition was paired with a baseline consisting of observation of geometrical objects (OGO), real or virtual, presented individually in repeated series. Four different geometrical objects were used: a sphere, a pyramid, a cube, and a block (see Fig. 1). The real grasping actions were performed by the

same actor, who provided the model for VR motor simulations (see below).

In the RE condition, the four geometrical objects were changed approximately every 3 s in counterbalanced randomized order across subjects, for a total average of 30 grasps for each sequence. Each VR sequence contained 44 grasps of 1.5 s each, interleaved with 0.5 s of blank. The duration of each sequence was 90 s.

In all conditions, level of luminance was controlled and two-thirds of the forearm and the hand grasping geometrical objects were shown. Each participant underwent 12 PET scans. There were three repetitions per task.

In the VR conditions, the participants wore stereo glasses (Crystal Eyes), required for stereo vision. The VR motion sequences were constructed on a R4400, 64 Mbyte RAM, 150 MHz SGI Indigo2, as follows (Figs. 1A, 1C, and 1E). First, a two-layered, 3D static model of the hand and the forearm was constructed (Badler, 2000). The inner layer represented a well-detailed model of the hand and forearm skeleton. It was composed of 16 articulated segments with a total of 27 degrees of freedom (*df*). Each finger was represented as a linked chain of three segments, except the thumb, which had two. This model allows flexion/extension of one segment with respect to the adjacent one. The fingers were attached to the palm through a joint which allowed both flexion/extension and abduction/adduction of the entire finger for a total of 4 *df* per finger (3 *df* for the thumb). The palm was made of a quadrilateral which allowed warping and rotation of the palm with respect to the forearm along two orthogonal axes. The forearm had no constraint on rotation/translation (6 *df*). The skeleton dimensions were the same as those of the actor performing the RE task.

This 3D skeleton was then “dressed” with an envelope (second layer) composed of a triangular mesh. This component represented the outer shape and color of the hand and forearm. The only difference between VRH and VRL models was the outer layer. In the VRL model, the mesh consisted of only 81 polygons without smoothing. Green color was applied to give the hand an alien aspect. In the VRH model, 1728 polygons were used with automatic smoothing; the skin and nail colors were matched to those of the actor. The VRH and VRL meshes were constructed from a model provided by Softimage and connected to the skeleton by associating its vertices to one or more skeleton joints. The model was then animated by recording the motion of an actor while he made the movements with a set of 18 small (5 mm diameter) retroreflective markers, positioned on the skin in correspondence to specific repere points (see following). The motion on the hand and forearm was captured at 100 Hz (Borghese *et al.*, 1990). To guarantee the maximum realism of the movement, a large number of markers were placed. On thumb and

index and middle fingers, markers were positioned in correspondence of each joint and finger tip (four markers for each finger and three for the thumb). On the fourth and little fingers, markers were placed only on the tips and the knuckles and the motion of the finger intermediate joints was computed through inverse kinematics. Two markers were put on the carpal epiphysis of the radio and ulna and one marker in correspondence to the elbow joint.

The animation was simply obtained by linking each marker to its position on the envelope: the marker motion drove the movement of the skeleton and the deformation/motion of the envelope. The final sequence was stored using a custom compression algorithm to achieve real-time animation at stereo full-screen resolution.

(2) In the second PET experiment, the subjects observed filmed motor sequences on a 21-in. TV screen (TV condition). These sequences were obtained by filming with a videocamera a real hand grasping geometrical objects, as in the first experiment. Exactly the same set-up of the RE condition was re-created. In particular, the grasping movements were performed by the same actor trained for the RE and VR tasks, and the same four geometrical objects (a sphere, a pyramid, a cube, and a block) were used. The baseline consisted in the observation of video sequences, in which these geometrical objects were filmed in static position (OGO). Each TV sequence contained 44 grasps of 1.5 s each, interleaved with 0.5 s of blank. The duration of each sequence was 90 s. Each participant underwent six PET scans. There were three repetitions per task.

Data Analysis

Image manipulations and statistical analysis were performed in MATLAB 4.2 (MathWorks, Natick, MA) using standard statistical parametric mapping procedures (SPM96, Wellcome Department of Cognitive Neurology, London, UK) (Friston *et al.*, 1995a; b). The data of all images were scaled to the grand mean value of 50 ml/s. A Gaussian filter ($16 \times 16 \times 16$ mm) was used. Only regional activations significant at $P < 0.001$ (corrected) were considered, except where noted (see below).

The simple main effects with baseline (RE-OGO, VRH-OGO, VRL-OGO) and direct comparisons between the experimental conditions (RE-VRH, RE-VRL, VRH-RE, VRL-RE) were designed to reveal differences in the activation foci associated with each experimental condition.

In addition, regions common to the experimental conditions were identified using the masking procedure in SPM. The procedure consists in masking a main effect with all related simple main effects. This eliminated voxels that were not significant at $P < 0.05$

in each contrast. Three statistical contrasts were performed to reveal the following commonalities:

1. All experimental conditions: (RE + VRL + VRH) – OGO masked with (RE-OGO), (VRH-OGO), (VRL-OGO).
2. RE and VRH conditions: (RE + VRH) – OGO masked with (RE-OGO), (VRH-OGO).
3. VRH and VRL conditions: (VRH + VRL) – OGO masked with (VRH-OGO), (VRL-OGO).

Finally, in order to investigate whether at a lower statistical threshold the RE and VR conditions shared some additional anatomical substrates, we explored at $P < 0.01$ (uncorrected). This procedure was applied in the contrasts (RE-OGO), (VRH-OGO), (VRL-OGO) and in the three analyses of commonalities (see below).

In the second experiment, the simple main effect (TV-OGO) was analyzed. Regional activations significant at $P < 0.001$ (corrected) were considered. We also explored this contrast at $P < 0.01$, in order to reveal possible activations overlapping with the activations found in the RE condition, which were not visible at the corrected significance level.

RESULTS

In the first experiment, we found commonalities but substantial differences in the pattern of activation among the tasks. Several bilateral foci were common to all the experimental conditions (RE, VRH, VRL), as revealed by the analysis of commonalities. These included MT (V5) and early visual areas close to the calcarine fissure, the fusiform gyrus, and cuneus. In the left hemisphere, there were additional foci in the parietal operculum, superior parietal lobule, and inferior temporal gyrus. When we analyzed the commonalities for RE and VRH conditions, we found common activations in the mesial premotor cortex (Ba 6) and the right superior parietal lobule (Ba 7), when the uncorrected significance threshold ($P < 0.01$) was applied. Activations common to VRH and VRL conditions were all located within associative occipital cortex, with a left side prevalence (see Table 1 and Figs. 2B and 2C).

The simple main effects with the baseline, while confirming the commonalities, revealed significant differences (Table 2 and Fig. 1). The RE condition selectively activated the precuneus (Ba 7) bilaterally and, in the right hemisphere, the inferior (Ba 40, 39) and superior (Ba 7) parietal lobules and the temporal pole (Ba 38). On the left, additional visuomotor structures were activated, namely the superior area 6 (mesial premotor cortex) and the cerebellum, the latter only at an uncorrected $P < 0.01$ significance threshold (see Table 2, in bold, and Fig. 2A). VRH and VRL conditions showed the bilateral involvement of occipital associative cortex

TABLE 1

Analyses of Commonalities between Conditions

Region (Ba) (<i>x,y,z</i> , and <i>Z</i> score)	RE	VRH	VRL
L MT (V5) (-48, -68, 4, 7.3)	+	+	+
R MT (V5) (52, -64, 0, 5.5)	+	+	+
L/R lingual/calcarine cortex (18/17) (-4, -86, -4, 6.8)	+	+	+
L parietal operculum (2/40) (-44, -34, 36, 4.2)	+	+	+
L superior parietal lobule (7) (-32, -58, 60, 4.6) (-18, -50, 64, 4.0)	+	+	+
L inferior temporal gyrus (20) (-48, -40, -20, 4.1)	+	+	+
L cuneus (18) (-22, -88, 24, 6.3)	+	+	+
R fusiform gyrus (37) (40, -50, -8, 4.1)	+	+	+
L mesial premotor (6)* (-14, 10, 64, 3.8)	+	+	
R superior parietal lobule (7)* (32, -52, 60, 4.1)	+	+	
L lingual gyrus (18) (-12, -78, -8, 6.9)		+	+
L superior occipital gyrus (19) (-30, -84, 28, 6.2)		+	+
L middle occipital gyrus (18) (-26, -90, 12, 6.8)		+	+
L inferior occipital gyrus (18) (-34, -90, 4, 6.0)		+	+
R inferior occipital gyrus (18) (34, -74, -8, 4.6)		+	+

Note. $P < 0.001$, Bonferroni corrected, except voxels marked by an asterisk, which survived an uncorrected $P < 0.01$.

(Ba 18, 19, 37) (see Table 2). At the uncorrected threshold ($P < 0.01$) there was an activation in the superior area 6 (mesial premotor cortex), comparable to the RE condition, and also for VRH condition.

The direct comparisons between the experimental conditions provided further clear-cut evidence of the condition-specific areas of activation (see Table 3).

In the second experiment, in which a TV screen was used for the observation of real hand movements, activation foci included area V5 bilaterally and other left visual regions, namely the cuneus (Ba 18) and the lingual gyrus/calcarine cortex (Ba 18/17). At a lower significance threshold ($P < 0.01$), the superior parietal lobule (Ba 7) and the parietal operculum (Ba 2/40) were also activated on the left (see Table 2).

DISCUSSION

Our study demonstrates different functional correlates for perceiving actions performed by a real hand in a real environment, in comparison with 3D virtual-reality and 2D TV hand motor sequences. The degree of realism in the reproduction of the VR hand seems to have limited effect, in particular in the engagement of right hemispheric structures.

Several bilateral foci were common to all the experimental conditions, including areas specialized for motion information processing (MT) (Watson *et al.*, 1993) and for attention to visual motion (early visual areas close to the calcarine fissure and cuneus), as recently shown by a fMRI study (Buchel and Friston, 1997).

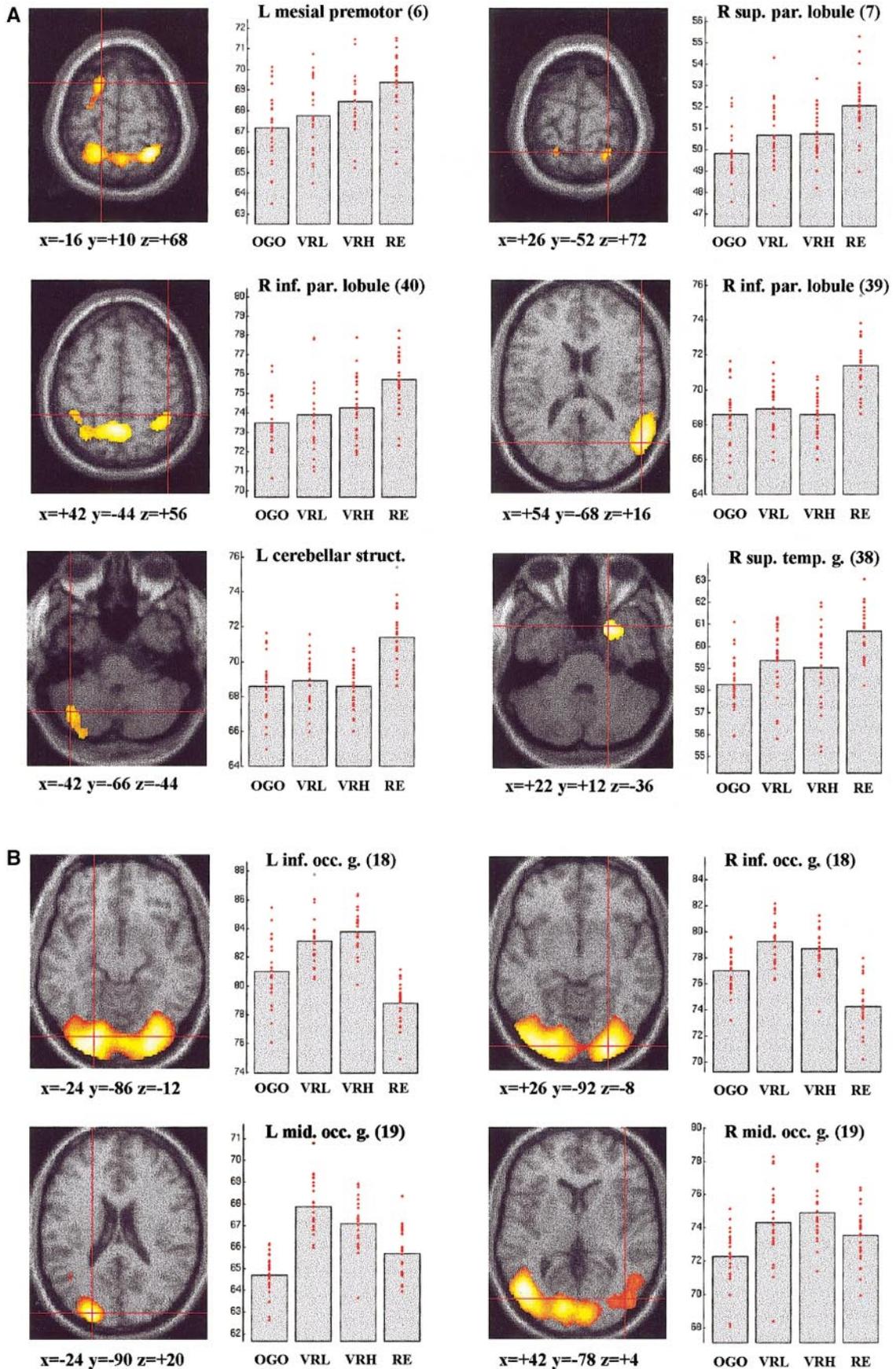
There were common activation foci in the posterior parietal cortex of the left hemisphere, which may mediate the visuospatial control of planning goal-directed actions (Milner and Goodale, 1996) and is also known to be associated with motor and spatial orienting attention (Nobre *et al.*, 1997). In monkeys, there is evidence that spatial representation of limb position, target location, and potential motor action are associated with neuronal activity in the posterior parietal cortex (Kalaska *et al.*, 1997). In addition, neural activities related to attention to actions and intention to act are also coded in the posterior parietal cortex, which may thus represent an interface between sensory and motor areas, in which cognitive functions related to sensory-motor transformation are coded (Andersen *et al.*, 1997).

Activation of the left parietal operculum was also common to all conditions: this is a sensory area and its activity might reflect reafferent proprioceptive signals triggered by the observation of object/hand-related actions (Iacoboni *et al.*, 1999).

We want to underline the fact that, since all the VR movements were recorded from real kinematics, they represented "biological motion," totally comparable to the real and TV hand motor sequences. Biological actions are a powerful stimulus for action programming, even if they are not followed by action execution. Thus, the common brain network shared by real, VR, and TV grasping actions could represent the neural encoding of biological motion. Recent PET experiments provided additional evidence showing that, within the pattern of movements perceived, only the biomechanically possible movements activated parietal brain structures related to motor processing (Bonda *et al.*, 1996; Stevens *et al.*, 2000). These results also provide new experimental evidence for the dominant role of lesions of the left hemisphere in producing ideomotor apraxia (De Renzi *et al.*, 1980).

The activation in the inferior temporal regions, shared by the RE and VR conditions, may represent the transformations carried out in the ventral stream to embody the perceptual and cognitive representation of actions (Decety *et al.*, 1997). Noteworthy, this activation was not present in the 2D TV condition, when the subjects did not receive three-dimensional information. These data further confirm recent results, in monkeys and humans, of three-dimensional shape coding in inferior temporal cortex (Janssen *et al.*, 2000a, b).

At a lower statistical threshold, two regions appeared to be shared only by RE and VRH conditions, namely the left mesial premotor region (Ba 6) and the right superior parietal lobule (Ba 7). These findings



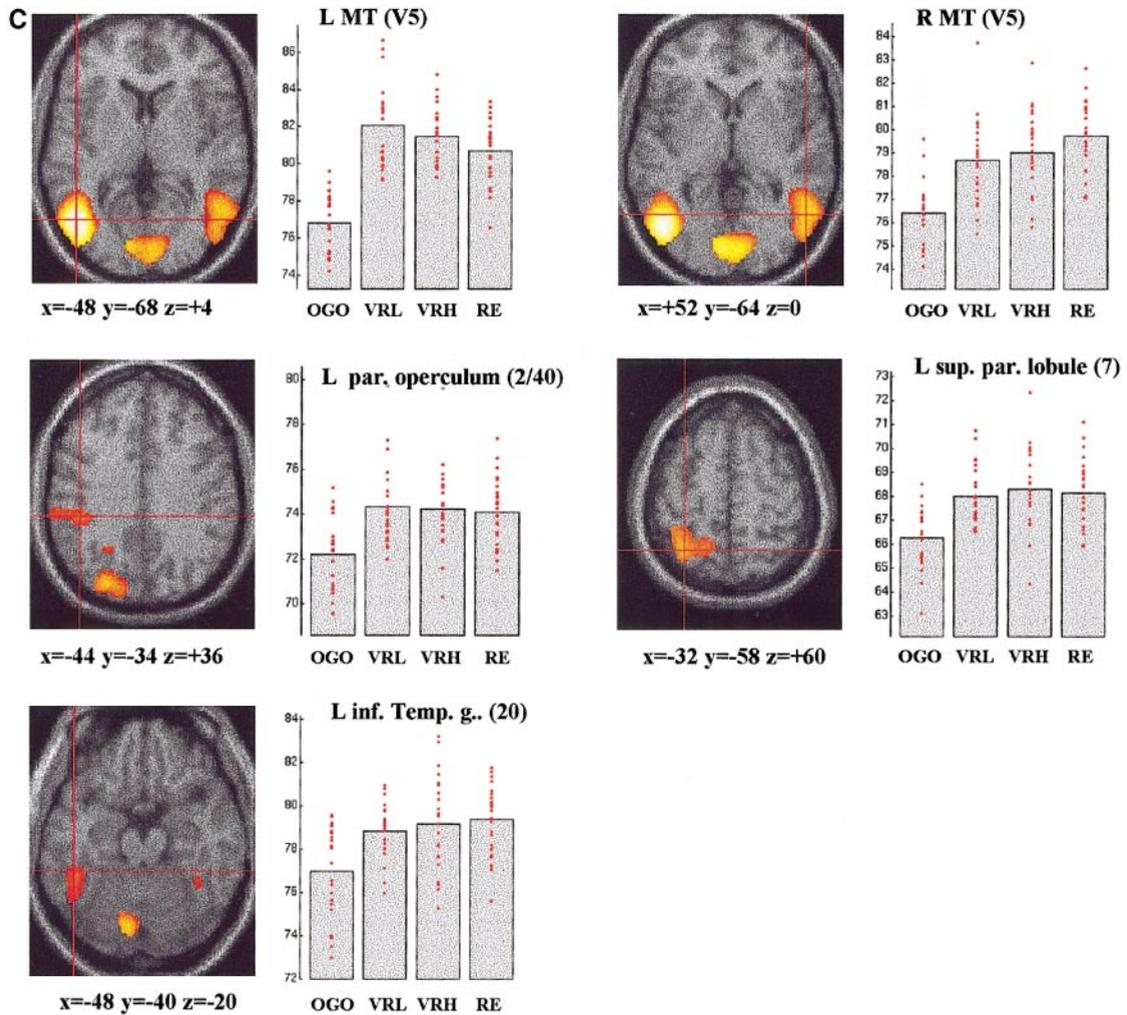


FIG. 2—Continued

suggest a possible role for the modulation of the quality of VR stimuli in partially matching to the neural systems underlying reality. Electrophysiological studies have recently confirmed the role of the mesial frontal system in dynamic representations that monitor and evaluate unfolding action plans (Luu *et al.*, 2000).

Prevalent visuoperceptual processes appear to be engaged when the actions are observed through simulated stimuli and space, such as in VR conditions. The common activated network included visual association areas that could be driven by the attended perceptual characteristics of VR stimuli, such as shapes and colors

of the reconstructed hands (Corbetta, 1993; Kourtzi and Kanwisher, 2000).

The selective involvement of the right inferior parietal cortex only in the real conditions is in agreement with several psychophysical experiments showing a right hemisphere superiority for visuospatial processes prior to movement (Chua *et al.*, 1992; Decety, 1996). In monkeys, the dorsal part of the inferior parietal lobule plays a crucial role in visually guided reaching and manipulation (Sakata *et al.*, 1997). Studies in humans confirm a role for this area when visual cues are used for motor planning (Deiber *et al.*, 1996). During the RE

FIG. 2. The areas of activation superimposed on axial views of a standard MRI image and histograms of the hemodynamic response in the corresponding foci are illustrated. Single activation voxels, as indicated by the intercept of the two orthogonal red lines, correspond to the stereotactic coordinates indicated below each axial slice (see also Tables 2 and 3). In the histograms, the ordinate indicates the adjusted regional cerebral blood flow values; the gray bars indicate the average values and the red points indicate the 24 PET scan measurements for each condition. Activation profiles are grouped in (A) for the RE condition and in (B) for the VR conditions. In (C) are grouped the activation profiles specific for the network encoding biological motion (see Discussion).

TABLE 2
Simple Main Effects

Region (Ba)	RE vs OGO (x, y, z, Z score)	VRH vs OGO (x, y, z, Z score)	VRL vs OGO (x, y, z, Z score)	TV vs OGO (x, y, z, Z score)
Mesial premotor (6), L	-16, 10, 68, 3.9	-12, 14, 64, 3.1*		
MT (V5)				
L	-50, -64, 8, 6.7	-48, -68, 4, 6.8	-48, -68, 4, 7.1	-48, -72, 4, 7.5
R	54, -62, 8, 6.2	50, -66, -4, 4.9	50, -66, -4, 4.2	52, -70, -4, 5.4
Lingual gyrus/calcarine cortex (18/17)				
L		-4, -86, -8, 6.9	-6, -86, -4, 6.7	-10, -88, -16, 4.9
R	8, -82, 0, 4.6	4, -90, -4, 6.6	14, -88, -4, 4.7	
Parietal operculum (2/40), L	-42, -38, 32, 3.6	-40, -34, 36, 3.7	-48, -30, 32, 3.8	-64, -26, 28, 3.2*
Cuneus (18/19), L	-12, -84, 36, 4.6	-22, -88, 24, 5.7	16, -96, 8, 4.4	-18, -86, 28, 3.5
Inferior temporal/fusiform gyrus (21/37), R	40, -64, -8, 3.8	40, -50, -8, 3.5	38, -50, -8, 3.9	
Superior parietal lobule (7)				
L	-32, -58, 60, 3.8	-32, -60, 56, 4.4	-34, -50, 60, 3.7	-30, -50, 60, 4.2
R	26, -52, 72, 4.8			
Inferior parietal lobule (39, 40)				
L	-50, -44, 28, 4.3	-26, -56, 36, 3.6		
R	-38, -42, 56, 3.7	-36, -48, 56, 3.9	-36, -42, 56, 3.8	
	60, -48, 20, 4.7			
	42, -44, 56, 3.8			
Precuneus (7), L/R	-2, -56, 52, 4.9			
	0, -66, 48, 4.4			
	22, 12, -36, 4.6			
Superior temporal gyrus (38), R				
Posterior fusiform gyrus (37)				
L		-46, -50, -24, 4.1		
R	24, -82, -16, 4.3	20, -80, -8, 4.5		
Middle occipital gyrus (19)				
L		-36, -82, 8, 5.6	-24, -90, 20, 7.0	-24, -92, 12, 4.0
R		42, -78, 4, 4.0	28, -96, 12, 3.3	
Inferior occipital gyrus (18), R		50, -76, 0, 4.3	50, -78, 0, 4.4	
		34, -74, -8, 4.5	34, -74, -8, 3.7	
Cerebellum, L	-14, -68, -48, 3.3*			

Note. $P < 0.001$, Bonferroni corrected, except voxels marked by an asterisk, which survived an uncorrected $P < 0.01$.

condition, subjects might have matched the real visuospatial pattern into motor plans associated with pre-existing visuospatial representations. These concern the relationships between external objects and the body of the observer within a "schema," which is qualified in terms of the specific frames of reference involved. Right inferior parietal lesions in humans are known to produce visuospatial deficits and spatial neglect, a condition which is associated with derangement of egocentric and allocentric coordinates (Bisiach, 1997). The present results are also consistent with neuroimaging evidence in normals of a crucial role of right parietal cortex in the visuomotor and spatial processing underlying the computation of egocentric spatial frame of reference (Burgess *et al.*, 1997; Vallar *et al.*, 1999). Similarly, studies in monkeys have implicated the inferior and posterior parietal cortex in the representations for body and world references (Snyder *et al.*, 1998).

Thus, the role of spatial reference frames may be crucial in differentiating the brain computations related to real versus VR or TV observed actions. It is possible that only within real environmental (periper-

sonal) space the right parietal system may provide nonretinocentric coordinates (egocentric and allocentric), related to the spatial representations necessary for high-order motor planning. The human neural substrate in motor observation might require a direct matching mechanism within the "actor" internal spatial representation. This mechanism is not available or experienced in simulated conditions, in which the perception-action mediation cannot rely on proper visuospatial representations. This is suggested also by a recent psychophysical experiment by Clower and Bousaoud (2000). Here, differences in adaptive responses to a prism displacing the visually perceived location of target objects were recorded, either when visuomotor feedback was provided in the reality or when it was provided on a virtual visual display. The results are discussed by the authors in terms of possible differences in the neural representations between artificial and normal visual environments.

Our data also suggest that the human brain has an "imprint" on visuomotor representations that derives from the acquisition of gesture recognition as long as it is performed by humans in a natural environment.

TABLE 3

Direct Comparisons

Region (Ba)	RE vs VRH (x, y, z, Z score)	RE vs VRL (x, y, z, Z score)	VRL vs RE (x, y, z, Z score)	VRH vs RE (x, y, z, Z score)
Superior parietal lobule (7), R		32, -52, 60, 3.6 22, -56, 68, 3.6		
Inferior parietal lobule (39, 40), R	54, -68, 16, 5.2 58, -56, 20, 5.1	62, -50, 24, 5.6 58, -56, 20, 5.3		
Precuneus (7) L		-10, -78, 52, 3.5 -2, -80, 44, 3.7		
R		4, -60, 60, 5.4 8, -66, 48, 4.5		
Superior temporal gyrus (38), R Lingual gyrus (18), R	30, 12, -32, 5.0		16, -98, -8, 5.9 8, -90, -12, 5.6	
Inferior occipital gyrus (18) L			-24, -86, -12, 7.0 -36, -92, -8, 6.9	-24, -90, -16, 6.5 -46, -80, -12, 6.0
R			28, -90, -12, 6.8 32, -82, 16, 6.5	26, -92, -8, 7.0 18, -100, -4, 6.0
Middle occipital gyrus (19), R				-34, -90, 4, 7.0 -26, -94, 12, 6.5
Cerebellar structures, L	-42, -66, -44, 4.0 -32, -84, -40, 3.8			

Note. $P < 0.001$, Bonferroni corrected.

Indeed, the ability to imitate actions of other persons has a fundamental role in the development of thinking and behavior in children. In agreement with our hypothesis are developmental studies showing that children can infer and understand actions, within a framework of goals and intentions, when the actions are performed by persons, but not by mechanical devices (Legerstee, 1991; Meltzoff, 1995).

Our results question the common belief that virtual reality (or 2D TV) can be used as an alternative to reality and suggest a novel criterion of assessment: the stimuli should be conceived as equivalent to real ones to the extent that they share a comparable neural network for their processing. This might also be of importance for researchers who contemplate the use of VR for functional imaging or neurophysiology experiments.

ACKNOWLEDGMENTS

We thank Dr. F. Perugini for production and delivery of radioisotopes, Dr. V. Blasi for help in data analysis, and Mrs. A. Comperchio for PET data acquisition.

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