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Does Perception of Biological Motion Rely on Specific Brain Regions?

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Perception of biological motions plays a major adaptive role in identifying, interpreting, and predicting the actions of others. It may therefore be hypothesized that the perception of biological motions is subserved by a specific neural network. Here we used fMRI to verify this hypothesis. In a group of 10 healthy volunteers, we explored the hemodynamic responses to seven types of visual motion displays: drifting random dots, random dot cube, random dot cube with masking elements, upright point-light walker, inverted point-light walker, upright point-light walker display with masking elements, and inverted point-light walker display with masking elements. A gradient in activation was observed in the occipitotemporal junction. The responses to rigid motion were localized posteriorly to those responses elicited by nonrigid motions. Our results demonstrate that in addition to the posterior portion of superior temporal sulcus, the left intraparietal cortex is involved in the perception of nonrigid biological motions. © 2001 Academic Press

Key Words: **fMRI; perception; biological motion; structure from motion.**

INTRODUCTION

As a social animal, a human's survival depends upon its ability to identify, to interpret and to predict the actions of others. Perception of other's motion, in particular, plays a major adaptive role. It may thus be hypothesized that the perception of biological motion is subserved by a specific neural network. Several decades of perceptual research support the idea that human observers are particularly sensitive to human movements. Early work performed by Johansson (1973) demonstrated that illuminating the joints of a walking individual suffices to convey a vivid, compelling impression of human animation, despite the percept collapsing into a meaningless stimulus when the walker stands still. Subsequent research has shown that our perception of the human form in such animated displays is extremely rapid (Johansson, 1976), orientation specific (Bertenthal and Pinto, 1994; Sumi, 1984), and extends to the perception of gender (Koslowski and Cutting, 1978), complex actions (Dittrich, 1993), social dispositions (MacArthur and Baron, 1983), and sign language (Poizner *et al.*, 1981). For these reasons, the perception of biological motion is hypothesized to represent an intrinsic capacity of the visual system. Evidence comes from experiments showing that infants 3 to 6 months of age already exhibit a preference for biological motion patterns (e.g., Fox and McDaniel, 1982; Bertenthal *et al.*, 1984).

The extremely rapid recognition of a few moving point-lights as depicting the human form suggests that the correct grouping of the point lights is accomplished early in visual processing (Johansson, 1973). Some psychophysical and computational models implicate low-level processing heuristics, such as local rigidity, to delimit the pair-wise connections of the point lights; these pair-wise connections are then iteratively combined into a hierarchically organized global form (Hoffman and Flinchbaugh, 1982; Webb and Aggarwal, 1982). Interestingly, subjects report viewing an emergent human form, rather than individual features or local relations making up this form (Bertenthal, 1993). One approach to determine whether the global structure of a moving point-light display depicting a human form can be perceived prior to the perception of the local relations is to interfere with the individual features by generating additional moving point-lights and adding them to the point-light display at random locations (Pomerantz, 1981). If the form is perceived globally, then the perception of a human figure should be unimpaired even though the perception of local relations is disrupted by the additional point-lights. Bertenthal and Pinto (1994) demonstrated that this is the case for an upright walker masked by additional point-lights, but subjects were unable to detect an upside-down masked walker. This latter finding suggests that the perception of the human form is orientation

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specific. Although the absolute motions of the inverted displays were identical to those of the upright displays, the relative motions were not organized into an emergent form that corresponded to the one that would be obtained from the ecological viewing of people performing actions. More recently, Thornton *et al.* (1998) performed a set of psychophysical studies suggesting that both low-level and high-level visual analyses are involved in the visual perception of human locomotion.

Where in the brain is biological motion processed? The visual cortex is organized into two neuroanatomically separate pathways, i.e., the ventral and dorsal streams. Ungerleider and Mishkin (1982) proposed that these pathways process information about "what" and "where," respectively. More recently, Milner and Goodale (1993) proposed a functional dissociation of these visual pathways according to their role in perception (ventral pathway) or in action (dorsal pathway), i.e., "what" vs "how." Accordingly, biological motion should be processed primarily by the ventral stream. Nevertheless, a review of recent findings suggests the involvement of a more complex network of cortical areas.

If we assume that the perception of biological motions is a special case of form-from-motion (FFM) or structure-from-motion (SFM), it becomes necessary to reevaluate our expectations about the processing of biological motions. Recent neurophysiological studies with monkeys reveal that areas MT/V5 and MST are directly involved in the extraction of 3-D structure-from-motion, and, in particular, in the segmentation and reconstruction of moving surfaces (Anderson and Bradley, 1998). This finding is difficult to reconcile with the view that the ventral pathway is exclusively responsible for processing information about objects, because both areas studied by Anderson and Bradley (1998) are located in the dorsal pathway.

Even if we assert that the perception of biological motions is a completely separate perceptual process, there is still evidence to challenge the position that these motions are processed exclusively by the ventral pathway. A series of neurophysiological studies in monkeys suggest that relatively high-level integrative mechanisms play a role in the visual analysis of actions. For example, Perrett *et al.* (1990) recorded in the superior temporal polysensory area (STP) of macaque monkeys, and reported that these neurons are attuned to precise combinations of primates' forms and movements. Also, these same neurons respond to Johansson point-light walker displays (Oram and Perrett, 1994). Based on these findings, it is difficult to exclude a contribution from the dorsal pathway because the STP receives input from both the dorsal and ventral pathways (Baizer *et al.*, 1991).

Studies involving humans with neurological lesions who are tested on the perception of biological motion are equally inconclusive. Some studies report the prominent role of the dorsal stream (Schenk and Zihl, 1997) while others emphasize the ventral stream (e.g., Vaina *et al.*, 1990; McLeod *et al.*, 1996). In addition, the patients examined by Vaina *et al.* (1990) and McLeod *et al.* (1996) were impaired in a low-level visual motion analysis task. Yet, these patients experience no difficulty in recognizing specific visual stimuli, i.e., biological human activities and geometrical objects, which both require the extraction of structure-from-motion.

Previous neuroimaging studies (Bonda *et al.*, 1996; Howard *et al.*, 1996) have addressed the perception of biological motions using point-light stimuli. However, they have not tested whether the perception of nonrigid (biological) motions, which is a particular case of structure-from-motion, and the extraction of rigid-structure-from motion is dissociable. This issue is of crucial importance in the light of neuropsychological observations that fail to dissociate these two types of motion processing (e.g., Vaina *et al.*, 1990; McLeod *et al.*, 1996).

In the present study, whole brain fMRI measurements were carried out in normal individuals while they were shown different motion displays including structure-from-nonrigid motion (biological), structure-from-rigid motion and drifting random dot displays. Our goals were (1) to determine if processing structure from nonrigid motion and rigid motions involve differences in their neural networks and to identify if there are unique neuroanatomical structures involved in the processing of biological motions and (2) to test the extent to which the neural network involved in the processing of high-level motion information (i.e., nonrigid and rigid motions) differs from the network involved in processing low-level motion information (i.e., drifting random dot displays).

MATERIAL AND METHODS

10 healthy right handed subjects (5 males and 5 females, mean age 24 ± 2 years) participated in this study which was approved by the Ethics Committee. All subjects gave their informed consent and were paid.

Activation Protocol

The stimuli presented were dot cinematograms depicting nonrigid biological motions, 3-D rigid motions of a rotating cube or drifting random dots. These cinematograms were generated by a computer and projected on a transparent screen positioned at the back of the magnet. Subjects viewed this screen by means of a mirror centered above the eyes. The cinematograms were 4.8° wide and 6° high, as viewed by the subjects. Each stimulus consisted of light gray elements (subtending a visual angle of 9.3 arc/min in width and 11.6 arc/min in height) moving against a dark background; stimuli were refreshed every 61 ms. Seven different types of stimuli were used:

1. Drifting random dot stimuli. One hundred fifty dots were used to create the drifting random dot display. The dots were randomly distributed with a probability density function of 10%. Dot velocity was approximately 2.5°/s. Eighty percent of the dots drifted either to the right or to the left while the remaining dots drifted in random directions. In order to ensure that individual elements would not be tracked, the dot lifetime (i.e., probability of a dot continuing along the same trajectory in the next frame) was set to 40%. Observers perceive these displays as 2-D surfaces drifting either to the right or to the left. This display was used as the baseline stimulus for assessing cortical activation to motion information.

2. Random dot cube. This display consisted of 20 random elements that moved as if they were located on the vertices and midpoints between vertices of a rotating cube. The cube was projected with perspective onto the screen along an axis that was slanted relative to the picture plane. It appeared to rotate either to the right or to the left at a velocity of 98°/s. This stimulus display subtended a visual angle of 2.3° in width and 2.9° in height.

3. Random dot cube with masking elements. A total of 37 masking elements were randomly distributed over the screen, and moved upwards or downwards at a velocity of 1.25°/s. These elements were superimposed onto the random dot cube creating a signal-to-noise ratio that was approximately the same as the signal-to-noise ratio used in the point-light walker displays (see below). The total number of elements in this display was 57. Note that the masking elements were identical to the target elements with regard to size and luminance.

4. Upright point-light walker. This stimulus consisted of 11 elements moving as if attached to the head and major joints of a person walking in place on a treadmill (Bertenthal and Kramer, 1984). It subtended a visual angle of 2.9° vertically and 2.3° horizontally at its fullest extension, and appeared to be walking either to the left or to the right along a path that was parallel to the picture plane. The point-light walker was programmed to step through a complete gait cycle every 40 frames. Unlike the random dot cube, the point-light walker was not globally rigid: individual limb segments moved simultaneously in opposite directions, and thus corresponded to a nonrigid stimulus.

5. Inverted point-light walker. This stimulus is identical to the preceding one, except that the target is inverted 180°. Initially, this display is more difficult to recognize as depicting a human form, but this difficulty doesn't usually persist once the display is recognized as a human form (Proffitt *et al.*, 1984).

6. Upright point-light walker with masking elements. This stimulus consisted of 22 masking moving elements distributed over the screen. The upright point-light walker display was superimposed in the middle of this region. Thus the total number of elements in this display was 33. The masking elements were generated by creating two identical sets of absolute motion vectors used in the walker display, but scrambling their spatial locations. Although the relative motions of these elements differed from those of the target because they were not spatially constrained, the elements were identical to those comprising the target with regard to size, luminance, and absolute motion.

7. Inverted point-light walker with masking elements. This stimulus is identical to the preceding one, except that the target and masking elements are presented upside down. As previously mentioned, the point-light walker target is not detected when the masked target is inverted, but it is detected when the masked target is upright (Bertenthal and Pinto, 1994).

Before the fMRI experiment began, subjects were familiarized with the experimental setup and short examples of each type of stimulus. Successive trials were presented for 2 s and separated by a 0.5-s intertrial interval. For each trial, subjects were requested to judge whether the target was moving toward the right or toward the left, or whether the walkers were facing right or left. Answers were provided by means of a two-key device. Each of the seven types of stimulus displays was presented in blocks of 12 consecutive trials with the order of the trial blocks randomized across subjects. This procedure was repeated until each subject was presented each type of stimulus for 9 blocks of trials (i.e., 108 stimuli of each type were presented). The direction of motion of the stimuli were randomized across trials but constrained to ensure that each block of trials consisted of six stimuli presenting motion to the right and six presenting motion to the left.

TABLE 1

Seven Scanning Conditions

Stimuli	Abbreviation
Random dots drifting to the left or to the right	R
Random dot cube rotating to the left or to the right	C
Random dot cube rotating to the left or to the right with masking elements	MC
Upright point-light walker facing to the left or to the right	W
Inverted point-light walker facing to the left or to the right	IW
Upright point-light walker facing to the left or to the right with masking elements	MW
Inverted point-light walker facing to the left or to the right with masking elements	MIW

Note. The task was identical in all conditions. Subjects were requested to judge whether the stimuli were moving toward the right or toward the left, or whether they were facing right or facing left (for the walkers).

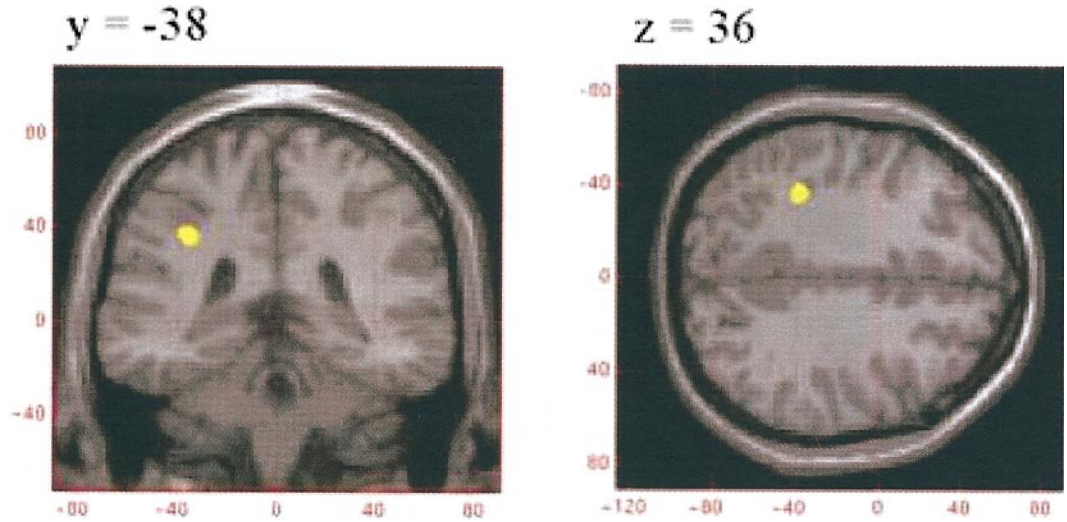


FIG. 1. Cluster in the left intraparietal sulcus (−36, −38, 36) found to be activated during the presentation of nonrigid biological motions stimuli. Voxels represented on the MNI template correspond to those voxels surviving to a threshold of 3 ($P < 0.01$) for the contrast (W+IW+MW+MIW)-2*(C+MC). The majority of these voxels belongs also to the intersection of contrasts W-R, IW-R, MW-R, and MIW-R.

MR Acquisition

Functional MR imaging was performed in a clinical setting, on a 1.5 Tesla MR imager (Philips NT). Thirty-two adjacent, axial slices (thickness 5 mm) were imaged sequentially. The imaging volume covered the subjects' whole brain and was oriented parallel to the bicommissural plane. Positioning of the image planes was performed on scout images acquired in the sagittal plane. A gradient-recalled echo EPI MR pulse sequence (GRE-EPI) was used. The following were the major MR acquisition parameters of this sequence: TR = 5 s, TE = 45 ms, flip angle = 90°, field-of-view = 256 × 256 mm^2, imaging matrix = 64 × 64. For each functional run, the seven conditions were randomly alternated with six scans per condition and repeated three times in a random order leading to a total of 126 volume acquisitions (acquisition time of 10 min and 30 s). Three functional runs were performed by each subject.

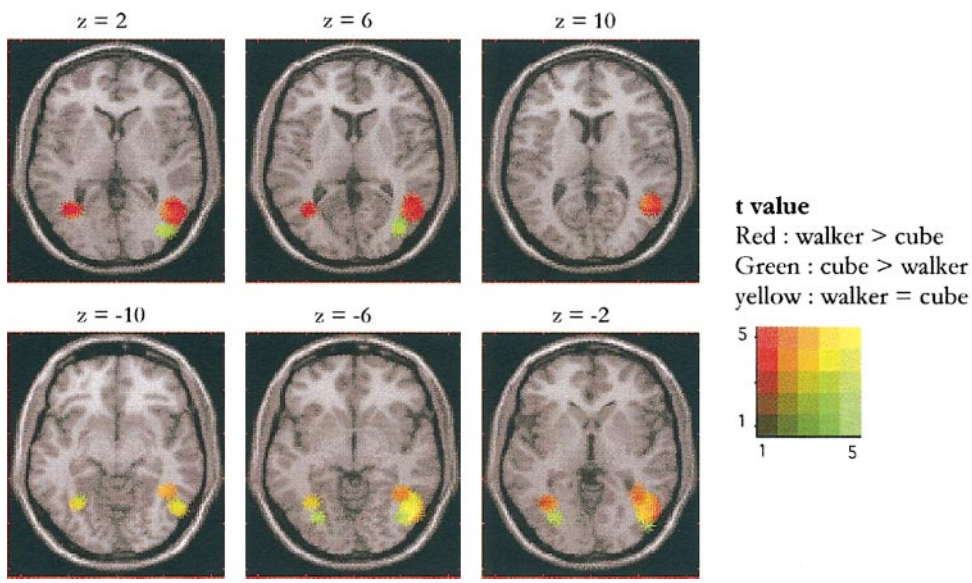
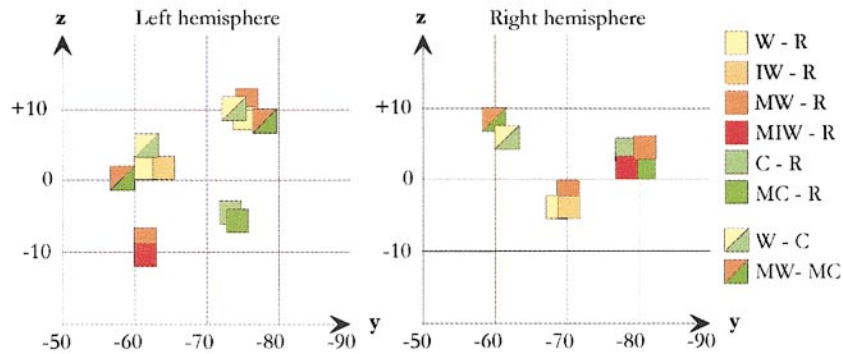


FIG. 3. Cerebral activations within the occipito-temporal region associated with the perception of point-light walker display or dot cube versus drifting random dots condition (W − R, C − R). Voxels displayed in color are superimposed on horizontal sections from the MNI template. Walker-responsive regions are in black-red spectrum, dot cube-responsive regions are in black-green spectrum. Finally, walker and cube-responsive regions are in black-yellow spectrum. Note that the walker responsive regions are localized anteriorly to the cube-responsive regions, yet they overlap.

A

	Left hemisphere					Right hemisphere				
Contrasts	x	y	z	t-level	extent	x	y	z	t-level	extent
W - R	-38	-62	2	6.41	58	48	-68	-4	8.28	505
	-34	-74	10	4.78	15					
IW - R	-36	-64	2	7.62	427	46	-70	-4	9.86	1165
MW - R	-36	-62	-8	9.92	978	48	-70	-2	10.92	3062
	-36	-76	10	7.56	120	38	-78	4	9.28	1201
MIW - R	-34	-62	-10	8.93	1046	38	-78	4	9.30	4213
C - R	-30	-74	-4	5.50	17	38	-78	4	6.06	46
MC - R	-30	-74	-4	5.61	31	40	-80	2	7.55	356
W - C	-38	-62	4	4.85	45	52	-62	6	5.10	305
	-34	-74	10	4.75	31					
MW - MC	-38	-58	0	6.23	255	54	-60	8	6.84	690
	-36	-78	8	6.77	98					



B

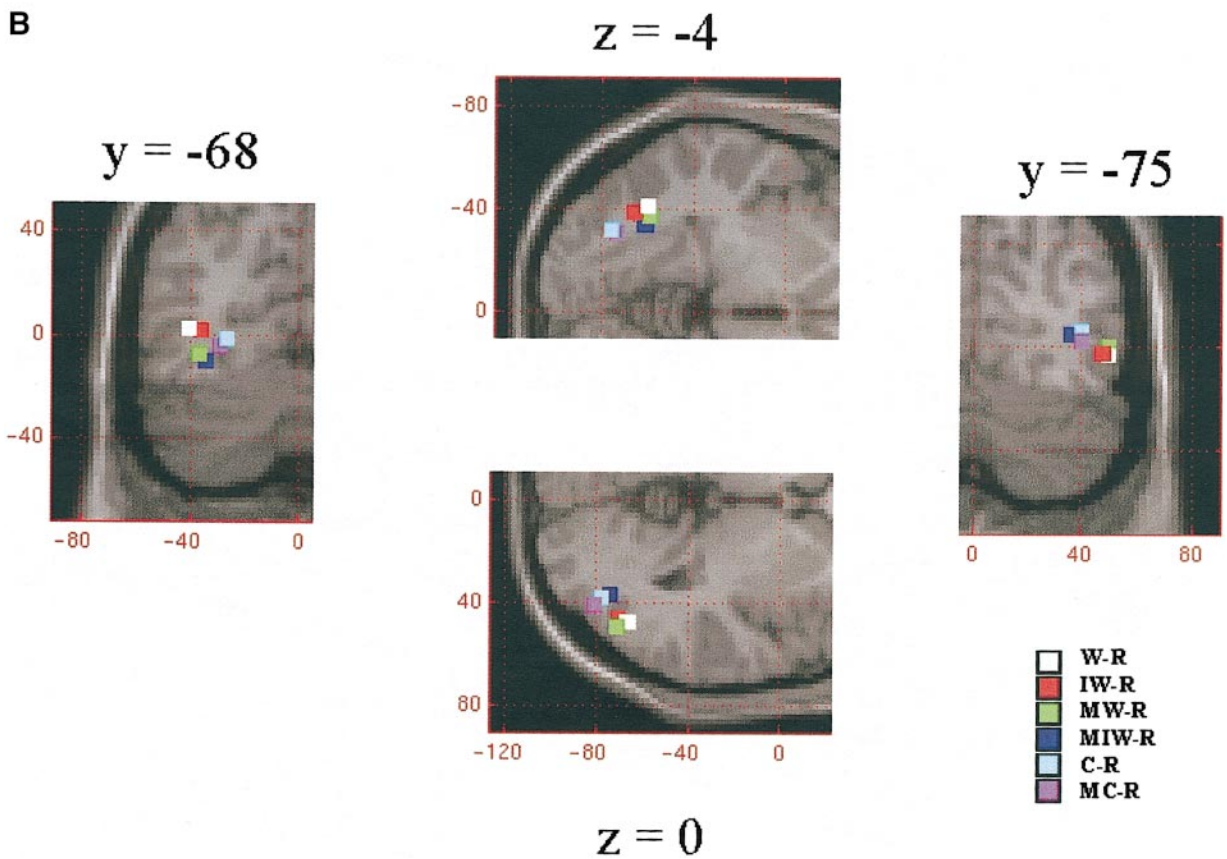


FIG. 4. Left and right hemispheric activations within the occipitotemporal region detected during each simple contrasts between target conditions and the drifting random dots condition or between a nonrigid motion condition (W or MW) and a rigid motion condition (C or MC). (A) Schematic representation and MNI coordinates Extent is given as number of voxels ($2 \times 2 \times 2$ mm). Note that in the right hemisphere, the masked walker conditions (MW and MIW) clustered with the cube and the masked cube, suggesting that they are not perceived as biological motions. (B) Illustration of the activity within the posterior part of the STS superimposed on the MNI MR template.

Subsequent to the functional MR scans, a high resolution 3-D T1-weighted MR scan was acquired from the volume functionally examined.

Planned Contrasts

1. To determine the neural network involved in the visual analysis of complex motion as compared to first order motion, a conjunction analysis was performed between the following contrasts: (i) Walker versus Random dots (W − R), (ii) Inverted walker versus Random dots (IW − R), (iii) Masked walker versus Random dots (MW − R), (iiii) Masked inverted walker versus Random dots (MIW − R), (iiiii) Cube display versus Random dots (C − R), (iiiiii) Masked cube versus Random dots (MC − R).

2. In order to determine how the extraction of form-from-motion for globally rigid (i.e., point-light cube) objects compares with that for semirigid (i.e., point-light walker) objects, the following contrasts were performed: (i) Walker versus cube (W − C); (ii) Cube versus walker (C − W), (iii) Masked walker versus masked cube (MW − MC), (iiii) Masked cube versus masked walker (MC − MW).

3. In order to test whether the processes involved in recognition of biological motion are orientation specific, the following contrasts were computed (i) Masked walker versus masked inverted walker (MW − MIW), (ii) Inverted masked walker versus masked walker (MIW − MW).

Data Analysis

The data were pre-processed with SPM 97 software (Wellcome Department of Cognitive Neurology, London, UK) and analyzed in Matlab. Motion correction of the functional images was applied with respect to a reference data set acquired halfway through the functional scans. The T1-weighted structural MRI scan for each subject was coregistered to the mean T2*-weighted images. The resultant structural images were then spatially normalized into a standard stereotaxic space, using as template a representative brain from the Montreal Neurological Institute. The parameters used for this transformation were applied to the functional images. This led to subsampling the image to a voxel size of 2 × 2 × 2 (original size 4 × 4 × 5 mm^3). Functional images were then smoothed with a 6 × 6 × 7.5 mm Gaussian kernel. Global activity for each scan was corrected by grand mean scaling. Low frequency signal changes were modeled, with a set of discrete cosine basis functions. Functional responses were determined using ANOVA. The condition, subject, conditions × subject interaction were estimated voxelwise according to the general linear model. In order to avoid having to model the hemodynamic response, the first two measurements within each condition were discarded. In addition, the four following scans were averaged to avoid correcting for correlation between scans. *F* values were calculated as the ratio of the variance between conditions and the variance related to the interaction term (subjects × conditions), because the factor "subject" was treated as a random factor. Voxels exhibiting a significant *F* value ($P < 0.001$) were submitted to further analysis: linear contrasts were assessed to identify the significant differences between conditions. The *P* values corresponding to Student *t* tests were corrected for multiple comparisons using the Scheffe method.

TABLE 2

Common Activated Foci Found in All Tasks as Compared to Baseline (Random Dots)

Brain Regions	MNI Stereotaxic coordinates			Extent
	x	*y*	*z*	
R Superior frontal gyrus/Precentral gyrus (FEF)	20	−8	58	13
R Superior bank of anterior IPS	34	−41	53	18
L Superior frontal gyrus/Precentral gyrus (FEF)	−20	−6	50	11
L Posterior SPL	−16	−65	46	13
R Postcentral gyrus	48	−25	40	20
L Postcentral gyrus	−54	−15	21	15
R MT/V5+	46	−70	−4	298
L MT/V5+	−34	−60	−9	31
L LOS/KO	−31	−73	−2	11
Cerebellum	13	−55	−23	17

Note. Intersection between all the activations obtained by calculating the contrasts W-R, IW-R, MW-R, MIW-R, C-R, MC-R (thresholds of $t = 3.00$). FEF: Frontal eye field; IPS: Intraparietal sulcus; SPL: Superior parietal lobule.

RESULTS

The perception of structure from motion, regardless of the type of visual motion was associated with increased activity in several sites, which are listed in Table 2, and include the intraparietal sulcus, the cerebellum, the superior frontal gyrus, the superior parietal lobule, the postcentral gyrus, and the MT/V5+ complex.

In order to identify the cortical activations elicited by the perception of biological motions (non rigid versus rigid), the following contrast ((1/2)*(W+IW+MW+MIW) − (C + MC)) was computed. In addition to the clusters that were detected in the first analysis (Table 2), a significant focus was found within the anterior intraparietal sulcus in the left hemisphere ($x = -36$, $y = -38$, $z = 36$; illustrated in Fig. 1).

The contrast between the walker (biological motion) and the cube (rigid motion) conditions led to three significant activations located bilaterally within the anterior part of the upper portion of MT/V5 complex

TABLE 3

Cortical Regions Found Activated for the Walker versus Cube Contrast
(Threshold of $t > 4.31$, $P < 0.001$, Extent > 10 Voxels)

Walker-cube	MNI Stereotaxic coordinates				
Brain regions	*x*	*y*	*z*	*t*-max	Extent
R ant MT/V5 complex	52	−60	6	6.41	190
L ant MT/V5 complex	−38	−62	4	5.22	13
L Intraoccipital sulcus	−34	−74	10	5.33	12

and within the left intra-occipital sulcus (Table 3). The locations of these foci are distinct from those found in the common network (intersection of activations found for the contrasts W-R, IW-R, MW-R, MIW-R). The same three regions are also found activated when considering the contrast MW-MC.

To test whether the perception of the walker is orientation specific, the upright walker condition was contrasted with the inverted walker condition (Table 4). For the W-IW contrast, activations were found within the left orbitofrontal and the left frontal pole as well as within the cingulate gyrus in the right hemisphere.

For the IW-W contrast, activations were located within the middle and inferior frontal gyrus, within the intra-occipital sulcus, and within the posterior part of the intraparietal sulcus in the right hemisphere. The precuneus, the superior parietal lobule and the posterior intraparietal sulcus were found to be activated in the left hemisphere.

From the behavioral measurements (RT and errors) as well as from the subjects' verbal reports, it appears that the masked (upright) walker was recognized while the masked inverted walker was not recognized (Fig. 2). Therefore, the comparison between these two conditions should reveal regions that correlate with the process of recognition. The right parahippocampal gyrus (38, −32, −18) was found activated for the MW − MIW contrast while left parahippocampal gyrus (−20, −24, −20) was activated for the reverse contrast (MIW − MW).

DISCUSSION

When comparing the six target conditions vs the baseline random dot condition (Table 2), activations located outside the visual areas were observed within the superior parietal, FEF, ventral premotor and prefrontal cortices. The involvement of this neural network has been well demonstrated both by neurophysiological experiments (e.g., Rizzolatti *et al.*, 1987; Sheliga *et al.*, 1994) and by neuroimaging studies and accounts for top-down attention modulatory influences from prefrontal to parietal and eventually to extrastriate cortex (e.g., Büchel *et al.*, 1998).

The main result of the present study is that the pattern of activation within the occipitotemporal junction is strongly influenced by the type of motion perceived both in terms of anatomical location and of extent, i.e., number of activated voxels. Activations were bilateral but were larger in extent and in terms of amount of activity in the right hemisphere, which is consistent with other recent findings showing right

TABLE 4

Cortical Regions Found Activated for the Walker vs Inverted Walker Contrast
(Threshold of $t > 4.31$, $P < 0.001$, Extent > 10 Voxels)

	MNI Stereotaxic coordinates				
Brain regions	*x*	*y*	*z*	*t* max	Extent
Walker—inverted walker					
L Orbitofrontal	−28	50	−26	5.43	35
L Mesial frontal pole	−6	42	40	5.06	40
R Cingulate gyrus	4	−20	38	6.85	47
Inverted walker—Walker					
R Inferior frontal gyrus	44	20	4	4.73	11
R Middle frontal gyrus	32	52	8	5.37	19
R Intra-occipital sulcus	40	−74	12	5.63	27
L Post IPS	−20	−82	20	5.47	24
R Post IPS	26	−70	40	6.34	258
L SPL/Precuneus	−16	−76	42	5.84	34
L SPL	−8	−66	54	5.34	13

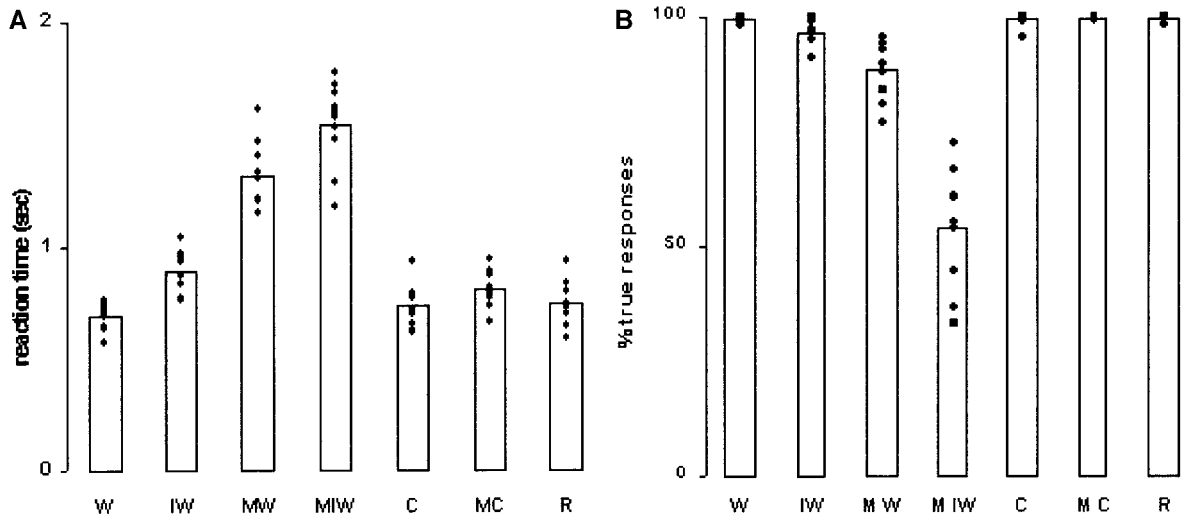


FIG. 2. Mean reaction time (A) and percentage of correct responses (B) according to the different conditions. Each point on the bars represents the mean value for one subject. As subjects were required to respond even when they did not recognize the form in motion, 50% of correct responses correspond to chance level.

hemispheric dominance for extracting depth from motion (Orban *et al.*, 1999; Grossman *et al.*, 2000). In addition, there was a clear functional segregation (Fig. 3) in the general neighborhood of the MT/V5 complex between nonrigid (biological) motion (activations located anteriorly) and rigid motion (activations located posteriorly). Recent results by Grossman *et al.* (2000) have shown that biological motions did not activate MT differently than scrambled biological motions, kinetic boundaries or coherent motion. Therefore, these biological motion activations observed in our study may correspond to the satellites of MT/V5 such as MST, and also to other neighboring regions such as the posterior part of STS or LOS/KO.

In the left hemisphere, three clusters were detected (Fig. 4). The two anterior clusters corresponded to nonrigid motion conditions and the posterior cluster corresponded to rigid motion conditions. It is not entirely clear where these clusters are located. However, recent findings provide evidence that they are localized in areas adjacent to MT/V5. For example, Grill-Spector *et al.* (1998) demonstrated that there is a convergence of visual cues in the lateral aspect of the occipital lobe (LO) during recognition of motion-defined object. In the original description of this large cortical region LOC, it was suggested that it is likely to be a complex of several areas (Malach *et al.*, 1995). In addition, Grill-Spector *et al.* (1998) have dissociated two putative subdivisions within this complex, the caudal-dorsal LO and the anterior-ventral PF/LOa. The posterior part LO is more sensitive to object transformations, whereas the PF/LOa shows sensitivity to different views of the same objects, particularly for faces (Grill-Spector *et al.*, 1998; Halgren *et al.*, 1999). Our results extend these findings by suggesting that there is also a segregation of activity within LOS/KO according to the type of motion-defined objects perceived (nonrigid versus rigid). In the left hemisphere, only walker and inverted walker conditions (recognized as human figures) are associated with a focus that is anterior and dorsal to the areas activated in response to the other stimuli (Fig. 4). The perception of biological movement of the whole body, the hand, and the eyes and mouth has consistently been reported to activate this region in the posterior superior temporal sulcus (Puce *et al.*, 1998; Bonda *et al.*, 1996; Decety and Grèzes, 1999). This region is also activated during the perception of still pictures of faces (Haxby *et al.*, 1999, 2000; Kanwhisher *et al.*, 1997; Halgren *et al.*, 1999; Chao *et al.*, 1999). This neural activity may reflect the role of this region in the perception of changeable aspects of the body (all parts) that vary with movements, and in its interpretation. Moreover, it may be the homologue to the STPa region in monkey where neurons specifically respond to human movements (Bruce *et al.*, 1981; Perrett *et al.*, 1989).

In the right hemisphere, two clusters of activation were detected in the occipitotemporal junction in all target conditions (see Table 2). However, the more anterior corresponded to conditions where biological motions were recognized (W, IW, MW), and the more posterior clusters corresponded to rigid motion conditions (C and MC) as well as to the masked biological motion conditions (MW and MIW) (see Fig. 4). Orban *et al.* (1999) have shown that, at similar coordinates ($x = 52$, $y = -62$, $z = -4$), 3-D stimuli yield stronger activation than corresponding 2-D stimuli, and that nonrigid stimuli activate this region more than their rigid counterparts. Our results suggest a difference in localization as well as amount of activation. The fact that

the masked inverted walker (and masked walker to a less extent) is clustered with rigid motion is consistent with the RTs data showing that the masked inverted walker is not recognized.

Due to the extent of the activation, and to the right hemisphere dominance of MT/V5 in extracting structure from motion, we cannot exclude the involvement of MT/V5 in addition to LOS/KO and STS, MT/V5 in the rigid motion conditions. Indeed, Andersen and Bradley (1998) have proposed that the area MT/V5 has a more elaborated than previously thought in extracting 3-D structure from motion perception.

Interestingly nonrigid biological motion conditions were associated with specific activations in the intraoccipital sulcus and in the anterior IPS in the left hemisphere (Fig. 4). The intraoccipital sulcus might correspond to V3a. It has been demonstrated that V3a shares connections with areas in both the temporal and the parietal cortex (e.g., Tootell *et al.*, 1997), which is also the case for STS (Boussaoud *et al.*, 1990; Harries and Perrett, 1991). Those regions have been found to be engaged during the perception of real actions (Grafton *et al.*, 1996; Grèzes *et al.*, 1998; Perani *et al.*, 2000) and may be considered to be involved during the perception of human movements.

When the biological motion stimuli were masked, specific left hemispheric activation was detected in the intraparietal sulcus extending to the superior parietal lobule. From clinical observation it is not clear as to the importance of the parietal cortex in the recognition of biological motions such as Johansson-like stimuli. Indeed, both Vaina *et al.* (1990) and MacLeod *et al.* (1996) have reported that patients with bilateral lesions of MT/V5 are able to recognize biological motion stimuli. However, Schenk and Zihl (1997) have demonstrated that only patients with bilateral lesions of the superior and inferior parietal lobes present a strong deficit in the processing of biological motion when masked. This latter observation is supported by our results.

The fact that the right parahippocampal gyrus was involved when the walker was recognized against the masking elements is consistent with previous neuropsychological observations (Leornard and Milner, 1991) as well as a neuroimaging study by Decety *et al.* (1997) that has shown the importance of this structure in action recognition. The left parahippocampal activation which occurs when the walker is not recognized support its involvement with novel stimuli (e.g., Schacter *et al.*, 1995).

CONCLUSION

The results from this study reveal significant and extensive hemodynamic responses to both rigid and nonrigid (biological) motions. These activations were localized primarily at the occipitotemporal junction, and likely included MT/V5, LOS/KO, and the posterior STS. It is noteworthy that the pattern of activation followed a gradient in which the responses to rigid motions were consistently localized posterior to those responses elicited by nonrigid (biological) motions. The perception of biological motions was specifically associated with responses in the posterior STS as well as the left anterior portion of the IPS. Future research will be needed to address whether any of these areas of activation are specific to the perception of biological motions or to nonrigid motions, more generally.

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