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Separate neural pathways for contour and biological-motion cues in motion-defined animal shapes

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Abstract

To determine whether contour and biological motion (BM) cues for motion-defined shapes are subserved by two separate mechanisms, we used PET to measure regional cerebral blood flow in nine human subjects. Subjects were scanned in the following four conditions: (1) contour-defined animals *with* natural movements (running), (2) motion-defined animals in which the contours were removed and dots were placed on the limbs and moving parts (BM; running); (3) drifting static animal shapes (contours); and (4) drifting dots. The results demonstrate that the perception of BM involves the superior frontal gyrus, the precuneus, the fusiform, the lingual and the medial temporal gyri, the inferior parietal lobe, the hippocampal and parahippocampal areas, and the cerebellum. In addition, the anterior cingulate cortex and the amygdala were significantly activated. The perception of contour-defined shapes produced significant elevation of rCBF in some areas similar to the BM condition, namely the fusiform, medial occipital, medial temporal, and lingual gyri. Only the occipital pole and the inferior temporal cortex were specifically activated by contour-defined shapes. These results are congruent with previous findings that the dorsal visual pathway is important for the perception of BM. They further support psychophysical results showing that contour and BM cues for motion-defined animal shapes are processed by independent channels.

Keywords: PET; Biological motion; Contours; Perception; Ventral pathway; Dorsal pathway

Introduction

The perception of actions performed by others forms a key feature to survival. The visual system is remarkably adept in recognizing activities performed by others even when the patterns of movement are impoverished by removing contours (BM). In their original study, Johansson (1973) attached small light sources to the points of articulation of a walking person and presented this display in darkness to remove all other visual information. This resulted in vivid impressions of a walking human. Subsequent studies, using the same types of display, further demonstrated that the perception of BM patterns can be used to discriminate gender and identity of familiar individuals (Cutting, 1978), forward and backward walking direction (Mather et al., 1992), ambulating mode (Bertenthal et al., 1984), complex actions (Dittrich, 1993), social dispositions (MacArthur and Baron, 1983), and sign language (Poizner et al., 1981). The perception of human form in such animated displays occurs extremely fast (Johansson, 1976), is orientation-specific (Bertenthal and Pinto, 1994), and starts at a very early age (3 to 6 months of age; Bertenthal et al., 1984; Fox and McDaniel, 1982). BM can also be perceived without access to local motion signals in both human (Beintema and Lappe, 2002) and animal shapes (second order information; Bellefeuille and Faubert, 1998).

Recent brain imaging studies using PET (Bonda et al., 1996; Grèzes et al., 1998) and fMRI (Puce et al., 1998; Grossman et al., 2000; Grèzes et al., 2001; Grossman and Blake, 2001) have shown that the perception of BM derived from animated human actions is located in the right poste-

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rior superior temporal sulcus (STS), although some have reported bilateral activations on the STS anterior to MT (Howard et al., 1996). Other sites of activation were found in the medial cerebellum (Grossman et al., 2000), the amygdala (Bonda et al., 1996), the frontal cortex, and the inferior temporal gyrus (Grèzes et al., 1998). More recently, studies using fMRI have shown strong BOLD signals in areas within the lingual gyrus at the cuneus border (Servos et al., 2002), in the lingual and fusiform gyri, and in the superior temporal sulcus (Vaina et al., 2001). While in the first study there was no overlap between BM detection and object recognition (Servos et al., 2002), the other showed that common areas were activated by both types of stimuli, indicating that the ventral and dorsal visual streams are activated by the recognition of biological motion stimuli (Vaina et al., 2001). Taken together, these data suggest, however, that BM is subserved by specific brain regions that are distinct from those involved in the perception of other types of motion.

The questions we wanted to address in this study are the following. First, do stimuli made out of motion-defined animal shapes activate the same areas as motion-defined human shapes? Psychophysical experiments showed that subjects can easily recognize animals on the basis of their BM patterns (dynamic displays) but not under a static condition (Mather and West, 1993; Bellefeuille and Faubert, 1998). The ability to interpret BM is thus not restricted to human movements but can be generalized to animals. Second, is there a dissociation between BM and contour cues concerning neural processing (dorsal vs ventral streams)? In the affirmative this would support psychophysical findings suggesting that motion-defined animal forms derived from contour cues are initially processed independently from animal shapes defined only by BM cues (Bellefeuille and Faubert, 1998).

Material and methods

Nine healthy volunteers, four males and five females (ages 25 to 32 years) participated in this study after giving written informed consent. Subjects were neurologically sound and their vision was excellent. The study protocol was approved by the Aarhus University Ethics Committee.

Stimuli

The same sequences used in Bellefeuille and Faubert (1998) were used for the present study. The shapes represented the movements of two types of animals (a horse and a greyhound dog). Five to eight images of each animal were chosen to represent characteristic types of motion. The stimulus background was composed of 50% black and 50% white random dots. Each dot consisted of a single pixel. During the presentation the shape traveled from the left of the screen to the right in a loop fashion. That is, when the animal disappeared at the right end, it would reappear on the left side and travel across the screen again. This pattern was cycled throughout the scanning period for all testing conditions. A single motion sequence across the screen (for all conditions) was composed of 16 displacements (frames) and each frame was presented for 0.045 s for a total sequence of 0.72 s, creating a motion speed of approximately 41°/s. There was a partial overlap of the frames in space.

As the images were presented, the random dots in the area defined by the elements reversed polarity; i.e., white dots became black and vice versa (second order motion). The total dot density and mean luminance of the image thus remained constant. Therefore, if motion was stopped (single frame or a static presentation) the foreground (i.e., elements composing the different cues) was indistinguishable from the background.

In the BM condition, dots were placed at the animal's limbs and moving parts (two dots on the tail, two dots on the head, one in the center of the back, and three dots on each leg). The contour thickness and the size of the dots were adjusted such that a similar number of pixels (same area) were generated for both conditions. For example, the horse in the contour condition contained approximately 8190 pixels whereas in the dot condition it contained 8220 pixels. Four motion conditions were created, two with the contour stimuli and two with the dot stimuli. In the contour condition with natural movement (running) (R+ctr), a series of frames representing a natural sequence of running motion were cycled (Fig. 1a). In the contour condition without natural movement (drifting contour), one frame was drifted across the screen (Fig. 1b). In the BM condition the series of frames were cycled representing natural movement (running) (Fig. 1c). Finally, in the condition without natural movement and without contour (drifting dots), one frame was traveled across the screen with the same spatiotemporal properties as in the other conditions (Fig. 1d). An example of this kind of second order animation can be found at the psychtoolbox demo page (http://psychtoolbox.org/intro.html). Stimuli were presented on a 21-inch monitor (Tektronix) positioned 57 cm from the subject's eyes in a dimly lit room and subtended 12° of visual angle. The entire adapting field was 35 × 43°. In all conditions the stimuli moved from left to right and were continuously tracked during scanning. With the speed and tracking demands being identical in all conditions, eye movement components should not contribute to differences in brain activation.

Procedure

Before being placed in the scanner, subjects were shown some samples of the stimuli and were asked to identify the animals in the contour conditions. They were then prepared for scanning (insertion of a fine needle catheter into the bracchial vein) and positioned in the scanner. They were instructed to track the stimuli moving across the screen and to verbally report their perception after each PET session.

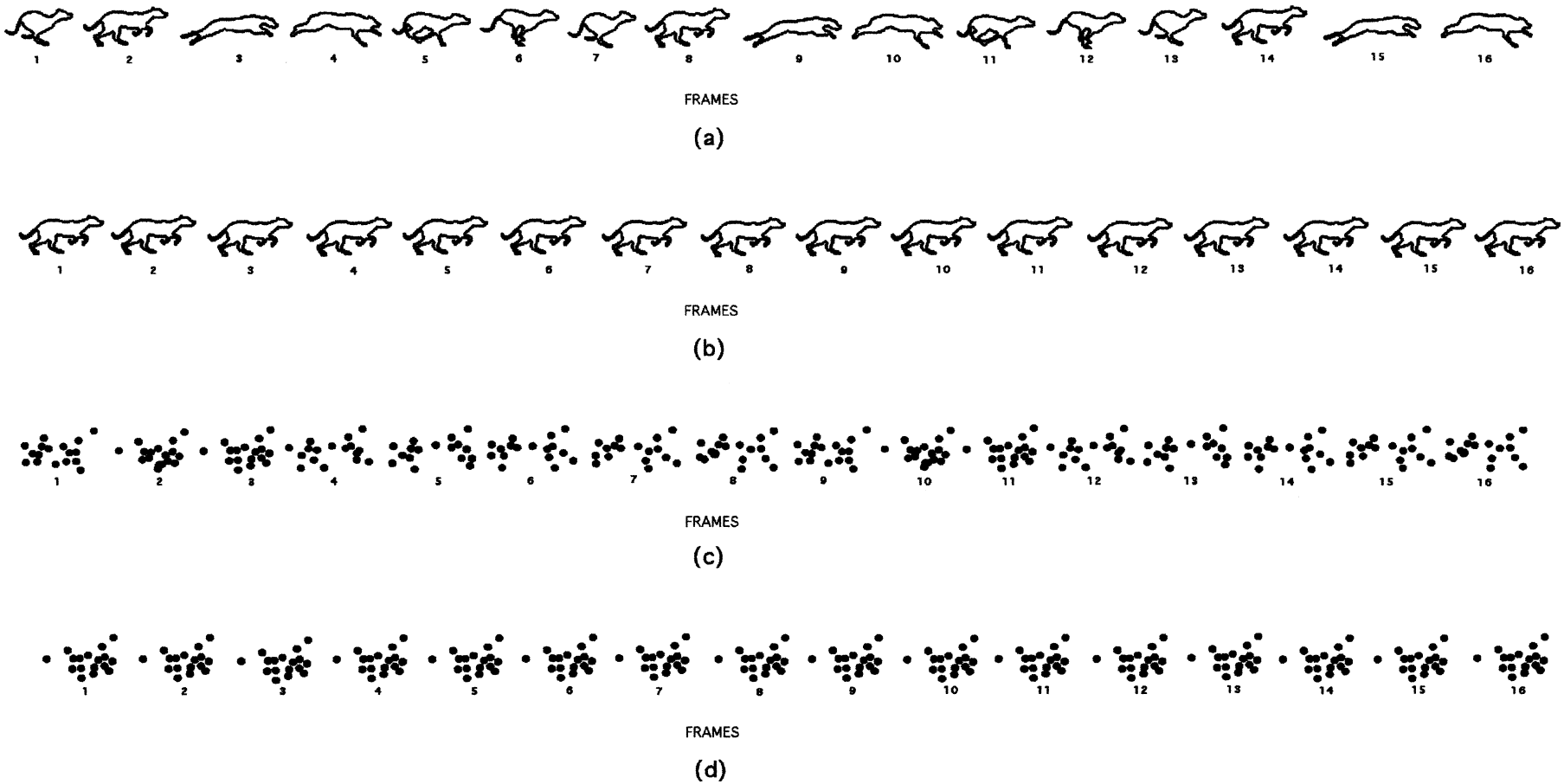

Fig. 1. Examples of the different motion conditions used in the experiment. (a) Contours with biological motion (animation of the 16 frames will produce a greyhound *running* across the screen); (b) contours without biological motion (animation of the 16 frames will produce a greyhound *drifting* across the screen); (c) dots with biological motion (animation of the 16 frames will produce a horse *galloping* across the screen); (d) dots without biological motion (animation of the 16 frames will produce dots *drifting* across the screen).

Table 1
Brain areas activated by biological motion and contour cues

Biomotion						Contour					
Area	Talairach Coordinates			*t*	*P*	Area	Talairach Coordinates			*t*	*P*
	x	*y*	*z*				*x*	*y*	*z*		
Superior frontal gyrus	3	58	15	5.0	0.00001	Inferior temporal gyrus	41	−61	−11	5.2	0.00001
Precuneus	−4	−50	45	4.7	0.0004	Fusiform gyrus	39	−47	−18	4.2	0.002
Anterior cingulate cortex	4	25	−6	4.2	0.002		37	−66	−18	3.9	0.02
Fusiform gyrus	27	−57	−15	3.8	0.007	Medial occipital gyrus	−42	−81	5	4.1	0.001
Medial temporal gyrus	−44	−26	0	3.8	0.017	Medial temporal gyrus	40	−69	15	3.2	0.040
	−56	−71	18	3.6	0.01	Lingual gyrus	26	−66	3	4.1	0.002
Cerebellum	−7	−43	−15	3.9	0.026	Occipital gyrus	43	−78	0	3.7	0.010
	−1	−62	−26	3.8	0.037		−39	−85	2	4.0	0.009
Hippocampal gyrus	−33	−21	−6	3.8	0.003						
Inferior parietal lobe	43	−25	32	3.3	0.03						
Parahippocampal gyrus	−34	−18	−5	3.0	0.04						
Lingual gyrus	17	−80	−2	3.2	0.04						
Amygdala	−18	−1	−30	2.8	0.02						

The experiment involved 12 sequential measurements (four conditions in a pseudorandomized order, each repeated three times) of rCBF during the presentation of the different motion stimuli.

PET data acquisition and image analysis

Cerebral blood flow was measured with an ECAT Exact HR47 PET camera (Siemens/CT1, Knoxville, TN) in 3D mode following intravenous bolus injections of 500 MBq of $H_2{}^{15}O$. A single 60-s frame was acquired, starting at 60,000 true counts/s. Successive scans were separated by at least 12 min. Visual stimulus presentation was started 10 s before tracer injection and was continued throughout the rest of the scanning time. The PET images were reconstructed after correction for scatter (Watson et al., 1996) and measured attenuation from a Ga-68 transmission scan. The 47 3.1-mm slices were filtered to 12-mm FWHM isotropic (Hanning filter cutoff frequency 15 cycles/s). PET volumes were re-aligned using the Automated Image Registration software to correct for head movements between the scans. The first PET image was co-registered with the subject's T1-weighted MRI brain volume (Collins et al., 1994) and mapped into standardized stereotaxic space (Talairach and Tournoux, 1988) using a nine-parameter affine transformation. Statistical *t* maps were calculated after a pixel-by-pixel subtraction of PET volumes (Worsley et al., 1992). *P* values for local maxima were based on the Euler characteristic and calculated according to the method described by Worsley et al. (1996).

Results

Biomotion cues

To identify the cortical structures associated with the perception of biological motion, the following comparisons between experimental conditions and control conditions were computed: running dots (BM) minus drifting dots and running animal shapes (R+ctr) minus drifting animal shapes (contour). These comparisons led to a number of activations (reported in Table 1), the most significant of which were located in the precuneus, the inferior parietal lobe, the fusiform, the lingual, and the medial temporal gyri. Significant sites of activations were also found in the superior frontal gyrus, the cerebellum and the hippocampal/parahippocampal areas, the anterior cingulate cortex, and the amygdala. Fig. 2A illustrates the cortical areas forming the dorsal visual pathway related to biomotion.

Contour cues

The following subtractions revealed the cortical areas involved in the processing of contour cues for shape recognition. Drifting animal shapes (contour) minus drifting dots yielded strong activations in the occipital gyrus, parts of the lingual and fusiform gyri, and the medial and the inferior part of the temporal lobe. When BM was cancelled out in the subtraction R+contour (running animal shapes) minus BM (running dots), sites of activation were observed in the occipital gyrus and the inferotemporal cortex (illustrated in Fig. 2B). The right hippocampus was also strongly activated in the contour condition. It is interesting to note that all subjects easily recognized and identified the running animal shapes with dots at the joints (BM), whereas they could not do it when the dots contained no BM cues (drifting dots). Fig. 2B illustrates the cortical areas forming the ventral visual pathway related to shape recognition.

Discussion

The present results lead to two major conclusions. First, the brain areas involved in the perception of biological

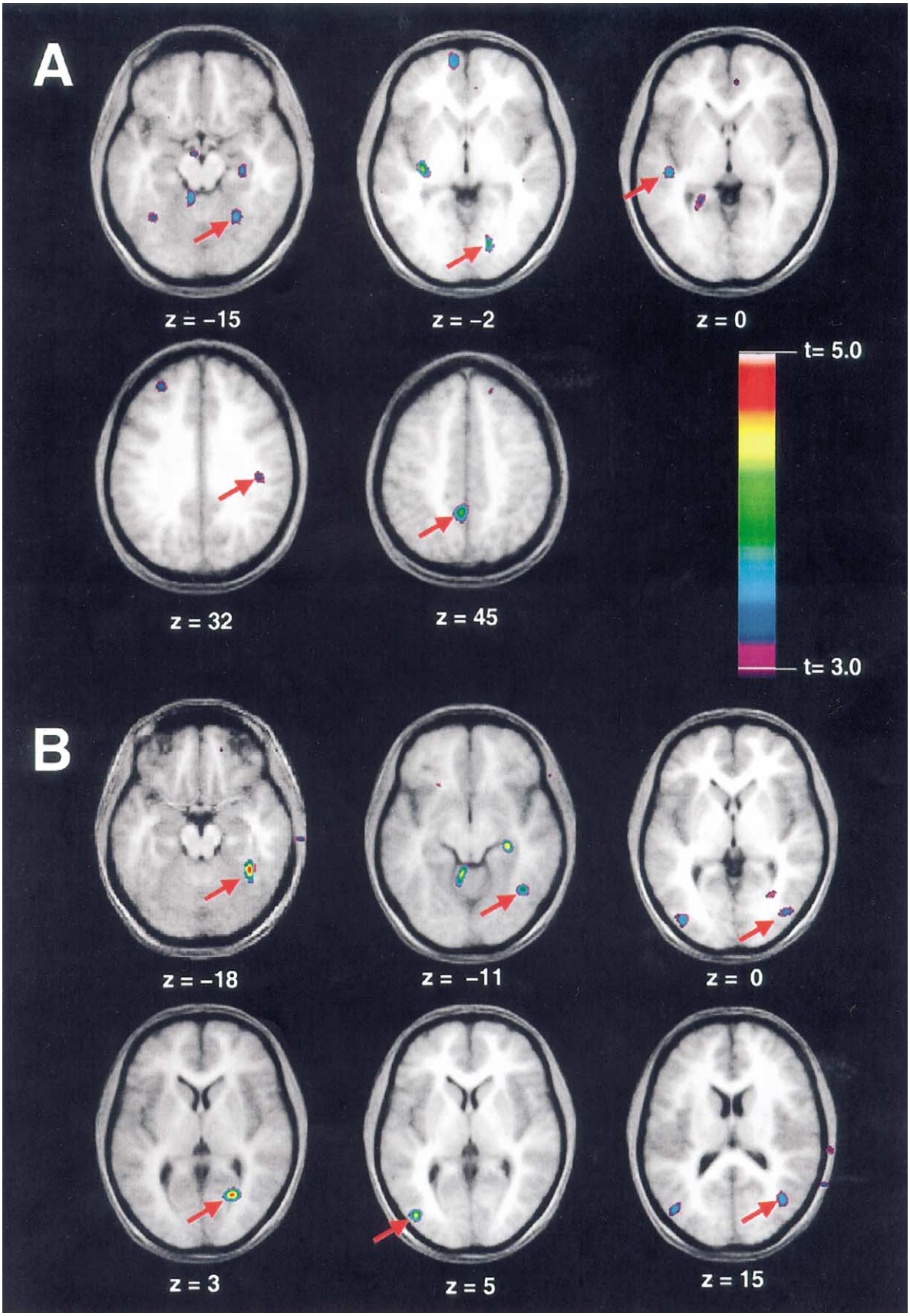

Fig. 2. Brain areas activated by biological motion (A) and contours (B). From left to right: (A) Fusiform gyrus (right); lingual gyrus (right); medial temporal gyrus (left); inferior parietal lobe (right); precuneus (left). Activation loci forming the dorsal visual pathway are indicated by the arrows. (B) Fusiform gyrus (right); inferior temporal gyrus (right); occipital gyrus (right); lingual gyrus (right); medial occipital gyrus (left); medial temporal gyrus (right). The loci of activation forming the ventral visual pathway are indicated by the arrows.

motion derived from animal shapes are similar to those for human forms. Second, biological motion cues (action-based form representation) are mainly processed in cortical structures belonging to the dorsal visual pathway, whereas contour cues (form representation) involve regions forming the ventral visual pathway. We found, however, that structures belonging to the dorsal stream were also activated by contour cues, suggesting that the recognition of biological motion stimuli may activate both systems. This result is in agreement with what has been reported by Vaina et al. (2001). When our subjects viewed biologically moving dots, they had a vivid impression of an animal running, whereas the stimulus became meaningless for drifting dots without BM cues. The loci of activation derived from such patterns (BM) were found in several cortical areas in both hemispheres and concerned mainly the superior frontal gyrus, the lingual and fusiform gyri, the precuneus, the superior and medial temporal gyri, the cerebellum, and the hippocampal formation. In the contour condition, strong activation was found in the occipital cortex and the inferior temporal gyrus. Activated areas, common to both types of stimuli, included the lingual, fusiform, and medial temporal gyri. Similar activation sites were reported for human forms and were located mainly in the posterior temporal sulcus and the left anterior portion of the intraparietal sulcus (Grèzes et al., 2001; Bonda et al., 1996; Grossman et al., 2000), the lingual and fusiform gyri and the STS (Servos et al., 2002; Vaina et al., 2001).

The parietal cortex is known to play a critical role in linking sensation and action (Goodale, 1997) and therefore is highly activated in most of the studies dealing with visual perception with intent to act. The intraparietal sulcus and the superior parietal lobule are involved not only in the execution and mental simulation of an action but also in its observation. This is in line with the suggestion that area BA 7 is involved in multimodal integration of external information and in visual attention. The passive observation of other's actions lead to activations of the temporoparietal junction (area V5) and the superior occipital gyrus (area V3), cortical areas known to respond to visual motion. Finally, the temporal lobe which is the final cortical stage (inferotemporal cortex) of the ventral stream plays a central role in the object recognition and categorization (Ungerleider and Mishkin, 1982). This region has been associated with the observation of hand action and is related to the analysis of biological motion. It thus seems to be a good overlap among action execution, simulation, and observation in the dorsal premotor cortex, the supramarginal gyrus, and the posterior parietal lobe. Observation of action, on the other hand, is associated with additional increase in rCBF in the ventral (temporal) pathway involved in the analysis of the visual scene. What has been overlooked is the strong cerebellar and hippocampal activations when subjects viewed biological motion sequences (Grèzes et al., 1998; Grossman et al., 2000). This has been ascribed to an overlap between neural systems involved in the planning of motor acts and those in the perception of motor activities.

Our results on biological motion with animal shapes taken in conjunction with those obtained using human forms indicate that there is a dissociation between the neural systems involved in the analysis of biological motion and form recognition. The dorsal visual pathway seems to be more involved with the analysis of the motion aspect of the stimulus (Ffytche et al., 1995; see review in Bremmer et al., 2000), whereas the ventral visual pathway is more concerned with form analysis (Ungerleider and Mishkin, 1982).

This dissociation between ventral and dorsal pathways has been supported by psychophysical and brain-lesion studies. Recently, Bellefeuille and Faubert (1998) have suggested at least two separate systems of analysis for form recognition that are independent from one another. One relies on the analysis of the contour and the other on biological motion characteristics to recognize form. Both lead to form recognition independently. Neuropsychological evidence also supports the presence of an independent system for action recognition. Patients with damage to motion areas of the dorsal stream are severely impaired in the perception of moving stimuli but can nonetheless perform normally on Johansson's (1973) biological motion task (Vaina et al., 1990; McLeod et al., 1996). Lassonde et al. (1993) studied two patients, one with a dorsal pathway lesion and the other with a ventral pathway lesion, who had intact global motion sensitivity. The ventral lesion patient could not identify static images of animals but could recognize them when they were animated in the same way as in the present study. The patient with the dorsal pathway lesion could not identify and discriminate any of the animated animals although he had no difficulty when they were presented in their static form.

Conclusion

The results of this study reveal that the observation of biological motion of animal sequences activates similar brain areas as those involved in the observation of human action. These activations were primarily localized in the extrastriate visual areas (such as areas V3 and V5), the cerebellum, the parietal lobe, and the inferotemporal cortex. It thus seems that both visual streams (dorsal and ventral) are involved in the analysis and processing of motion-defined shapes: the dorsal pathway mainly concerned with the BM cues for form representation whereas the ventral pathway is involved in the contour cues for form representation.

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