

Lesions to the Motor System Affect Action Perception

Andrea Serino^{1,2}, Laura De Filippo², Chiara Casavecchia²,
Michela Coccia³, Maggie Shiffrar⁴, and Elisabetta Làdavas^{1,2}

Abstract

■ Several studies have shown that the motor system is involved in action perception, suggesting that action concepts are represented through sensory–motor processes. Such conclusions imply that motor system impairments should diminish action perception. To test this hypothesis, a group of 10 brain-damaged patients with hemiplegia (specifically, a lesion at the motor system that affected the contralesional arm) viewed point-light displays of arm gestures and attempted to name each gesture. To create the dynamic stimuli, patients individually performed simple gestures with their unaffected arm while being videotaped. The videotapes were converted into point-light animations. Each action was presented as it had been performed, that is, as having been produced by the observer's unaffected arm, and in its mirror reversed orientation, that is, as having been produced by the observer's hemiplegic arm. Action recognition accuracy by patients with hemiplegia was compared with that by 8 brain-damaged patients without any motor deficit and by 10 healthy controls. Overall, performance was better in control

observers than in patients. Most importantly, performance by hemiplegic patients, but not by nonhemiplegic patients and controls, varied systematically as a function of the observed limb. Action recognition was best when hemiplegic patients viewed actions that appeared to have been performed by their unaffected arm. Action recognition performance dropped significantly when hemiplegic patients viewed actions that appeared to have been produced with their hemiplegic arm or the corresponding arm of another person. The results of a control study involving the recognition of point-light defined animals in motion indicate that a generic deficit to visual and cognitive functions cannot account for this laterality-specific deficit in action recognition. Taken together, these results suggest that motor cortex impairment decreases visual sensitivity to human action. Specifically, when a cortical lesion renders an observer incapable of performing an observed action, action perception is compromised, possibly by a failure to map the observed action onto the observer's contralesional hemisoma. ■

INTRODUCTION

Recent theories in cognitive neuroscience suggest that sensory and motor systems participate in conceptual processing (e.g., Martin, 2007). In particular, it has been proposed that action understanding is mediated by the same sensory–motor processes that are involved in action performance (Gallese, 2007; Rizzolatti & Craighero, 2004). The principal evidential basis for this view is that the motor system is automatically engaged when individuals observe the actions of others (see Iacoboni & Dapretto, 2006; Rizzolatti & Craighero, 2004 for reviews). The link between action performance and perception is further supported by behavioral evidence that an observer's motor activity influences their perception of other people's actions (Jacobs & Shiffrar, 2005; Hamilton, Wolpert, & Frith, 2004; Reed & Farah, 1995; see Blake & Shiffrar, 2007; Schutz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005 for reviews). In close

agreement, it has been shown that congenital deficits to peripheral sensory (Bosbach, Cole, Prinz, & Knoblich, 2005) and motor (Pavlova, Staudt, Sokolov, Birbaumer, & Krageloh-Mann, 2003) systems and body schema (Funk, Shiffrar, & Brugger, 2005) affect action perception. Finally, recent studies have shown that deficit in action planning, such as ideomotor apraxia, can affect not only execution of one's own gestures but also discrimination of other persons' gestures (Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008; Pazzaglia, Smania, Corato, & Aglioti, 2008; Buxbaum, Kyle, & Menon, 2005). Taken together, these findings suggest that the conceptual representations involved in action perception overlap with the sensory–motor representations used during action planning and execution, suggesting that action concepts are represented within the motor system. More specifically, it has been proposed that action perception is based on an automatic remapping—or an implicit simulation—of an observed action onto a motor representation of the same action in the observer's motor system. This view has been called simulation theory (Gallese & Goldman, 1998).

Although numerous studies have demonstrated clear associations between action perception and action production, a causal link remains to be identified. That is, in both monkeys and humans, it remains unknown whether a

¹Università degli Studi di Bologna, Bologna, Italy, ²CsrNC, Centro di studi e ricerche in Neuroscienze Cognitive, Polo Scientifico-Didattico di Cesena, Italy, ³Clinica di Neuroriabilitazione, Azienda Ospedali Riuniti Lancisi-Salesi-Umberto I, Ancona, Italy, ⁴Rutgers University, Newark, NJ

specific lesion of the motor system affects action comprehension (Mahon & Caramazza, 2008). Nonetheless, simulation theory clearly predicts that, to the extent that the motor system is necessary for action understanding, then patients affected by an elementary motor impairment due to brain damage should show some deficit in their perceptual analysis of other people's actions. Hemiplegia provides a stringent test of this prediction. Hemiplegia is the paralysis of one side of the body that results from a lesion at the motor system in the contralateral hemisphere. If action comprehension requires a remapping of an observed action onto the observer's own motor system, then an observer with hemiplegia should have a deficit in processing visually presented actions, and, more striking, such deficit could be more severe when processing actions performed with limbs attributable to the hemiplegic side of their body than when processing actions performed with limbs attributable to the uncompromised side of their body.

EXPERIMENT 1: RECOGNITION OF HUMAN ACTION

To test this prediction, 10 brain-damaged patients with paralysis of the contralesional upper limb (H+ group) after unilateral stroke were tested with an action recognition task. Their performance was compared to that of 10 healthy control observers and of 8 brain-damaged patients (H- group), who had suffered stroke, presented a comparable level of cognitive functioning as H+ patient, but did not present any motor deficits at the time of testing. The experimental stimuli consisted of degraded or point-light depictions (Johansson, 1973) of various arm gestures that the patients had previously produced with their unaffected arm and that the control participants had previously produced with either their right or left arm. Each point-light movie was displayed in two different orientations. In half of the trials, limb actions appeared as originally performed, that is, as performed with the arm on the patient's unaffected side of the body (real movement condition, Real-MC). In the other half of the trials, the point-light movies were mirror reversed or flipped about the vertical axis so that the identical actions appeared to have been performed with the arm on the patients' hemiplegic side (flipped movement condition, Flip-MC). Participants viewed both types of movies and attempted to verbally name each depicted action. According to simulation based theories of action comprehension (e.g., Gallese & Goldman, 1998), hemiplegic observers should be better able to recognize actions performed by the unaffected side of their body than actions performed by the hemiplegic side of their body. Indeed, visuomotor mapping of actions should be more strongly impaired when patients view actions attributable to their hemiplegic side of body. No such laterality effects would be expected neither with healthy controls nor with non-hemiplegic patients.

We used point-light displays, instead of fully rendered displays, to ensure that action processing was dependent upon kinematics cues, rather than any other perceptual or contextual cues. Dynamic point-light displays depict only the relative motions of a small number of markers that indicate the locations of the actor's major joints and head. All other visual information is erased (Johansson, 1973). This technique is widely used to study action perception (see Blake & Shiffrar, 2007, for a review) and observation of point-light animations of actions is sufficient to activate the same sensory-motor systems that are activated during the observation of whole-body actions (Ulloa & Pineda, 2007; Saygin, Wilson, Hagler, Bates, & Sereno, 2004).

To ensure that our action recognition task triggered automatic visuomotor mapping, a control condition with inverted point-light displays was also run. Inversion, or flipping about the horizontal axis, significantly disrupts the perception of human action in point-light displays (Blake & Shiffrar, 2007) presumably because observers are no longer able to directly map the perceived actions onto their motor representations, but they need to transform them into the corresponding upright views. With mapping disrupted, a dramatic performance decrease is expected when patients and controls view inverted depictions of the real and flipped point-light movies. Furthermore, and even more importantly, no laterality effect is expected when patients view inverted actions attributable to either the hemiplegic or unaffected side of their body.

The Role of Self-related Information

Watching someone performing an action provides visual information about the type of action as well as the type of individual (Daprati, Wriessnegger, & Lacquaniti, 2007a, 2007b; Troje, Westhoff, & Lavrov, 2005). In the present study, we also investigated how kinematic cues to identity influence action perception. If viewing an action automatically generates an internal simulation of the viewed action in the observer's motor system, then viewing one's own actions should induce the strongest possible visuomotor resonance because self-generated movements must logically produce the maximum overlap between visual and motor representations of actions (Loula, Prasad, Harber, & Shiffrar, 2005). Thus, another aim of the present research was to determine how self-related visual information affects action processing in patients with a damaged motor system. To that end, the point-light movies described above were arranged so that, for each subject from H+ patients group and healthy controls, one third of experimental trials depicted self-generated actions and the other two-thirds depicted actions performed by other people. To ensure that task performance differences would not be attributable to differences in the motor kinematics between brain-damaged patients and healthy subjects, hemiplegic patients saw movies of point-light actions performed by hemiplegic patients (themselves and two other patients), whereas controls saw movies of

point-light actions performed by controls (again, themselves and two other healthy controls). Participants received no information about the identities of point-light defined actors. Accuracy in the action recognition task was compared for self- and other-generated actions. If the visual perception of self-generated movement implicitly enhances visuomotor remapping, then superior performance in the action recognition task should be found when observers view their own actions.

Methods

Participants

Patients. Eighteen patients were recruited at the neuro-rehabilitation unit of the Ospedali Riuniti in Ancona, Italy, and volunteered to participate in this study. Patients had suffered a cerebrovascular brain lesion, as documented by a standard neurological examination and neuroradiological (CT or MRI scan) data, at least 6 months before participating in the study.

Exclusion criteria were (a) presence of widespread mental deterioration (Mini-Mental State Examination: cutoff score 24) or psychiatric disorders; (b) arousal or behavioral control inadequate for a 90-min experimental session; (c) hemispatial neglect and hemianopia; (d) global aphasia; or (e) apraxia. Patients showing hemianopia, hemispatial neglect, global aphasia, or apraxia were excluded from the study because these deficits may affect their perception of the visual stimuli, their ability to perform actions, their comprehension of the experimental tasks, and/or their motor responsiveness to the tasks.

Before the experiment, patients underwent a battery of neuropsychological tests. Each patient's general cognitive state was assessed with the Mini-Mental State examination test (Folstein, Folstein, & McHugh, 1975), hemispatial neglect with the Bell Cancellation test (Gauthier, Dehaut, & Joannette, 1989), hemianopia with the clinical confrontation test, and apraxia with the Test for Ideomotor Apraxia (De Renzi, Motti, & Nichelli, 1980). Patients' motor function was evaluated by an expert neurophysiologist. Motricity Index (Collin & Wade, 1990) scores for whole body and for the hand were recorded. Deep somatosensory sensitivity (pallesthesia) was also evaluated by a standard neurological method.

Patients were divided in two groups according to their motor abilities: Patients presenting unilateral hemiplegia of the upper limb, as documented by a standard neurological examination and neuroradiological data, were included in the H+ group (10 patients, 4 women). Motor functioning scales, reported in Table 1, confirmed the presence of unilateral hemiplegia. Patients who did not present motor deficits, as assessed by a standard neurological examination and confirmed by functioning scales, showing ceiling scores for all motor capacity measures (see Table 1), were included in the H- group (8 patients, 4 women).

H+ and H- patients were matched for age (mean = 56 and 59 years, respectively; $p = .77$), time from illness (41 and 37 months; $p = .80$) and general cognitive level (MMSE, H+ = 28; H- = 27; $p = .44$). Patients' demographic and clinical details are presented in Table 1.

Patients' brain lesions. Patients' brain lesions were identified in the MRI scans by an experienced neuroradiologist for all patients but two (Case 10 for H+ group and Case 8 for H- group, for whom only the medical report of the original CT scan was available). From the H+ group, six patients exhibited brain damage in their right hemisphere and four in their left hemisphere (RBD and LBD, respectively), whereas from the H- group, two patients exhibited a right brain damage and six a left brain damage. Brain lesions were drawn onto a normalized MNI template (www.bic.mni.mcgill.ca/cgi/icbm_view) using MRICro (www.mricro.com; Rorden & Brett, 2000). Subsequently, the locations of the lesions were identified using the Automated Anatomical Labelling map (Tzourio-Mazoyer et al., 2002) provided by the software, and with reference to the atlas of Duvernoy, Malm, Thuomas, Larsson, and Hansson (1991). Table 2 reports the anatomical structures and the Brodmann's areas (BA) damaged in each patient. Figure 1 shows lesion reconstructions for H+ patients and Figure 2 for H- patients.

All H+ patients suffered a lesion in the motor system, involving fronto-parietal motor circuits, basal ganglia, and/or corticospinal fibers of the internal capsule. H- patients suffered a lesion sparing the motor system, in that it was produced by strokes at a more posterior division of the medial central artery. Patients from both groups presented temporal and parietal lesions, involving BA 20–22 and BA 37–40, but only patients from H+ group presented frontal lesions involving BA 6, 8 and BA 44, 45.

Controls. Ten neurologically healthy subjects (4 men) matched for age (mean = 54 years) were also tested.

All subjects gave their informed consent to participate to the experiment, which was approved by the local ethical committee and was in accordance to the Declaration of Helsinki.

Stimuli

During the stimulus construction phase, H+ patients and healthy participants were individually seated on a darkened stage and videotaped as they performed a series of 10 actions with one of their upper limbs. Before videotaping, 12 reflective white markers were attached to the tight black clothes worn by each participant. The markers were systematically positioned on the major joints of the upper limb (5 markers on the fingers, 2 on the wrist, 2 on the elbow, 1 on the shoulder), the torso (1 marker), and the forehead (1 marker) as illustrated in Figure 2. The camera was fixed at a distance of 2.5 m directly

Table 1. Clinical and Demographic Data from Hemiplegic (H+) and Nonhemiplegic (H-) Patients

Case	Age	Sex	Months from Lesion Onset	Motricity Index		Pallesthesia	MMSE	Bell Cancellation Stimuli		Visual Confrontation Task			Apraxia Test Equivalent Scores
				Body	Upper Limb			Left	Right	Left	Right	Bilateral	
H+ 1	48	Male	6	0	0	0	28	14	17	10/10	10/10	10/10	4
H+ 2	56	Male	31	9	0	6	30	15	17	10/10	10/10	10/10	4
H+ 3	61	Female	19	38	14	6	30	17	17	10/10	10/10	10/10	4
H+ 4	37	Male	41	14	0	6	29	17	17	10/10	9/10	6/10	4
H+ 5	60	Male	112	33	0	6	26	16	14	10/10	10/10	10/10	4
H+ 6	57	Male	18	19	9	5	29	17	17	10/10	10/10	10/10	4
H+ 7	67	Male	33	28	9	5	29	16	17	10/10	10/10	10/10	4
H+ 8	65	Female	6	9	0	6	25	14	16	10/10	10/10	10/10	4
H+ 9	68	Female	8	0	0	6	24	17	17	10/10	10/10	10/10	4
H+ 10	66	Female	136	0	0	5	28	16	16	10/10	10/10	10/10	4
H- 1	51	Female	24	100	100	6	29	12	13	10/10	10/10	10/10	4
H- 2	61	Male	24	100	100	6	27	17	17	10/10	10/10	10/10	4
H- 3	70	Female	84	100	100	6	29	16	16	10/10	10/10	10/10	4
H- 4	57	Male	18	100	100	6	27	17	17	10/10	10/10	10/10	4
H- 5	46	Female	7	100	100	6	30	13	14	10/10	10/10	10/10	4
H- 6	56	Male	60	100	100	5	27	14	17	10/10	10/10	10/10	4
H- 7	58	Male	36	100	100	6	25	17	17	10/10	10/10	10/10	4
H- 8	80	Female	48	100	100	6	24	14	14	10/10	10/10	10/10	4

The Motricity Index scores for the level of hemiparesis varies from 0 (*paralysis*) to 100 (*normal strength*); any score <100 indicates a motor deficit. Pallesthesia scores vary from 0 to 8; scores <6 indicate an impairment. For MMSE scores, the range is 0 to 30 with a score <24 indicating impaired cognition. In Bell cancellation, range score is 0 to 17 cancelled items per side: a left/right differential score <20% on accuracy determined the presence of neglect. Apraxia test scores are presented as equivalent scores, varying from 0 to 4, whereby 0 defines a pathological performance and 2, 3, and 4 a completely normal performance.

Table 2. H+ and H- Patients' Lesions Sites in Brodmann's Areas and Subcortical Regions

<i>Case</i>	<i>Lesion Site</i>	
	<i>Hemisphere</i>	<i>Areas</i>
H+ 1	Right	BA 20–21; 34; 37; 45; 47; basal ganglia; thalamus
H+ 2	Right	BA 3, 6, 8, 9, 38, 40–47; basal ganglia; thalamus
H+ 3	Right	basal ganglia; thalamus
H+ 4	Left	BA 20–22; BA 37–45; basal ganglia; thalamus
H+ 5	Right	basal ganglia
H+ 6	Left	basal ganglia; thalamus
H+ 7	Left	BA 20–22; 37–38; basal ganglia; thalamus
H+ 8	Right	basal ganglia; thalamus
H+ 9	Left	BA 20–22; 37–38; 41–42; 44–45; basal ganglia
H+ 10	Right	parietal lobe; frontal lobe; basal ganglia
H- 1	Left	basal ganglia; thalamus
H- 2	Left	BA 20, 21, 37
H- 3	Right	BA 37; cerebellum
H- 4	Left	BA 37–39, 20, 21
H- 5	Left	BA 21, 40, 41
H- 6	Left	BA 21, 22, 37
H- 7	Left	BA 21, 22, 37
H- 8	Right	temporal lobe

in front of each actor. Participants performed each of the 10 actions five times. Each action lasted at least 5 sec and began from a standard position in which the subjects rested their hand on their ipsilateral leg. Half of the control subjects performed the action with their right hand and half with their left hand. All patients used their non-affected hand. There were two classes of actions: transitive (i.e., pantomimes using an object) and intransitive (actions with symbolic meaning that did not involve tool use). Transitive actions included hammering, handling a bottle with a power grip, using a key to open a door lock, writing, and smoking a cigarette. Intransitive actions included waving hello, moving the index finger left–right to mean “no” (depicted in Figure 3), repeatedly making the sign of the cross, tapping one’s index finger on one’s temple to mean “this is crazy,” and sending a kiss with the hand. Although the experimenter modeled each action, each actor was instructed to move naturally. This filming session lasted about 15 min.

The resultant digital videotapes were processed with professional video editing software to produce Johansson’s (1973) classic point-light displays. That is, everything was removed from each movie frame except the markers. As a result, each movie depicted only the movements of the 12 white markers against a homogeneous black back-

ground. Graphical editing also assured that all actors appeared to be the same absolute height and width within each movie so that gross cues to static body shape could not be used to recognize the agent of the action. The duration of each action movie was fixed at 5 sec. From the total sample of five versions of each action, three point-light movies were randomly selected for each of the 10 different actions per participant. The aim of this selection was to obtain a sufficient number of trials per condition, avoiding that the total experiment lasted too long. The other two movies, excluded from this selection, were used as practice trials (see below).

This resulted in the creation of a digital library of 30 movies for each of the 28 participants. As illustrated in Figure 2, the movies in this library were manipulated to create four types of trials. The veridical, unaltered movies constituted the real movement condition (Real-MC). Mirror-reversed versions of these movies, that is, movies created by flipping each veridical movie about the vertical axis, constituted the flipped movement condition (Flip-MC). Thus, the identical action appeared to have been produced by two different arms in the two trial types. Furthermore, inverted or upside-down versions of these two types of movies (I-RMC and I-FMC) were created by flipping the movies about the horizontal axis (Figure 3).

Experimental Task: Design and Procedure

At least 1 month after the stimulus construction session, participants were invited back to complete the testing

phase. The 1-month delay was employed to minimize the likelihood that participants would remember the specific movements that they had performed during the filming. During the experiment, participants were presented with

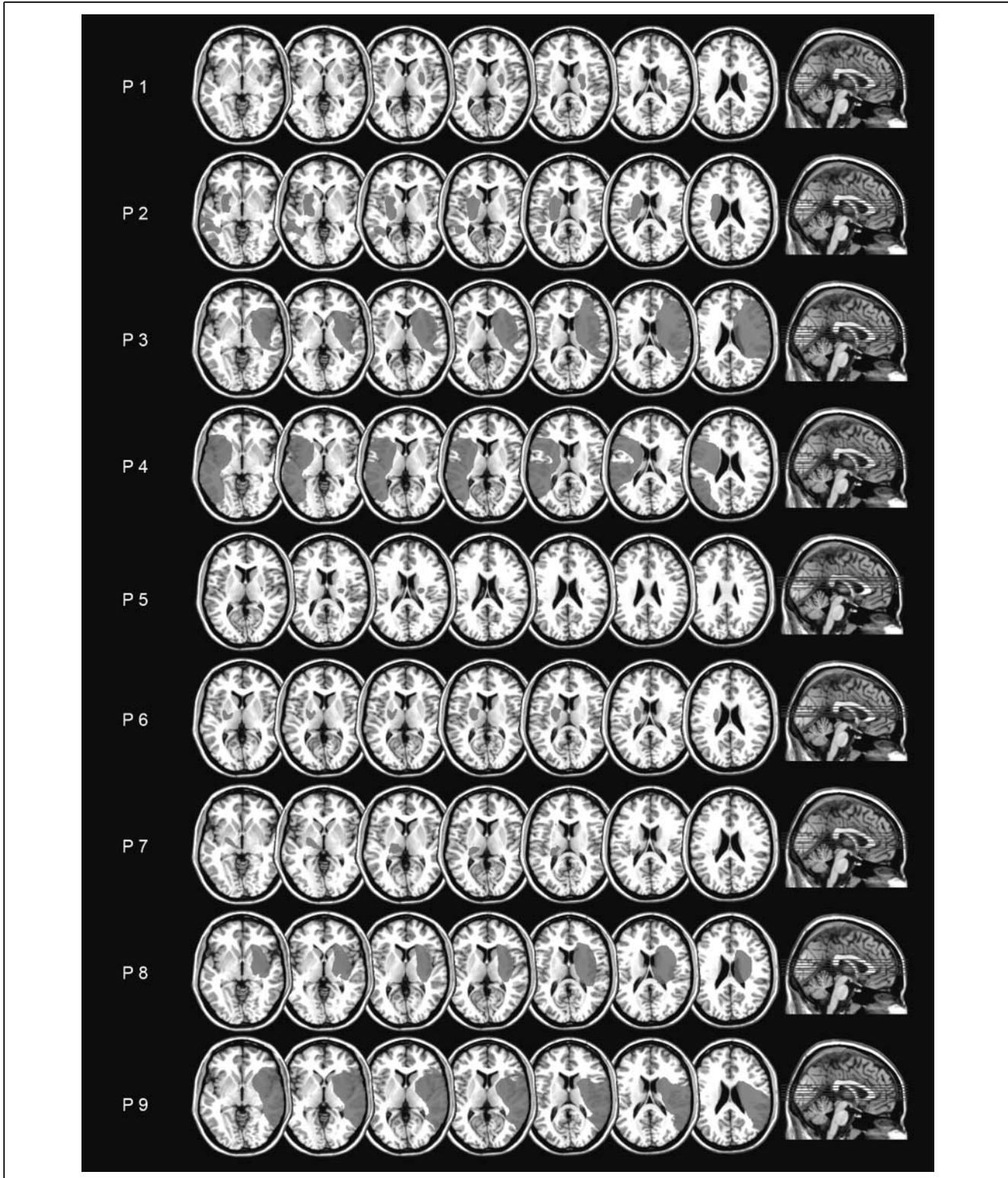
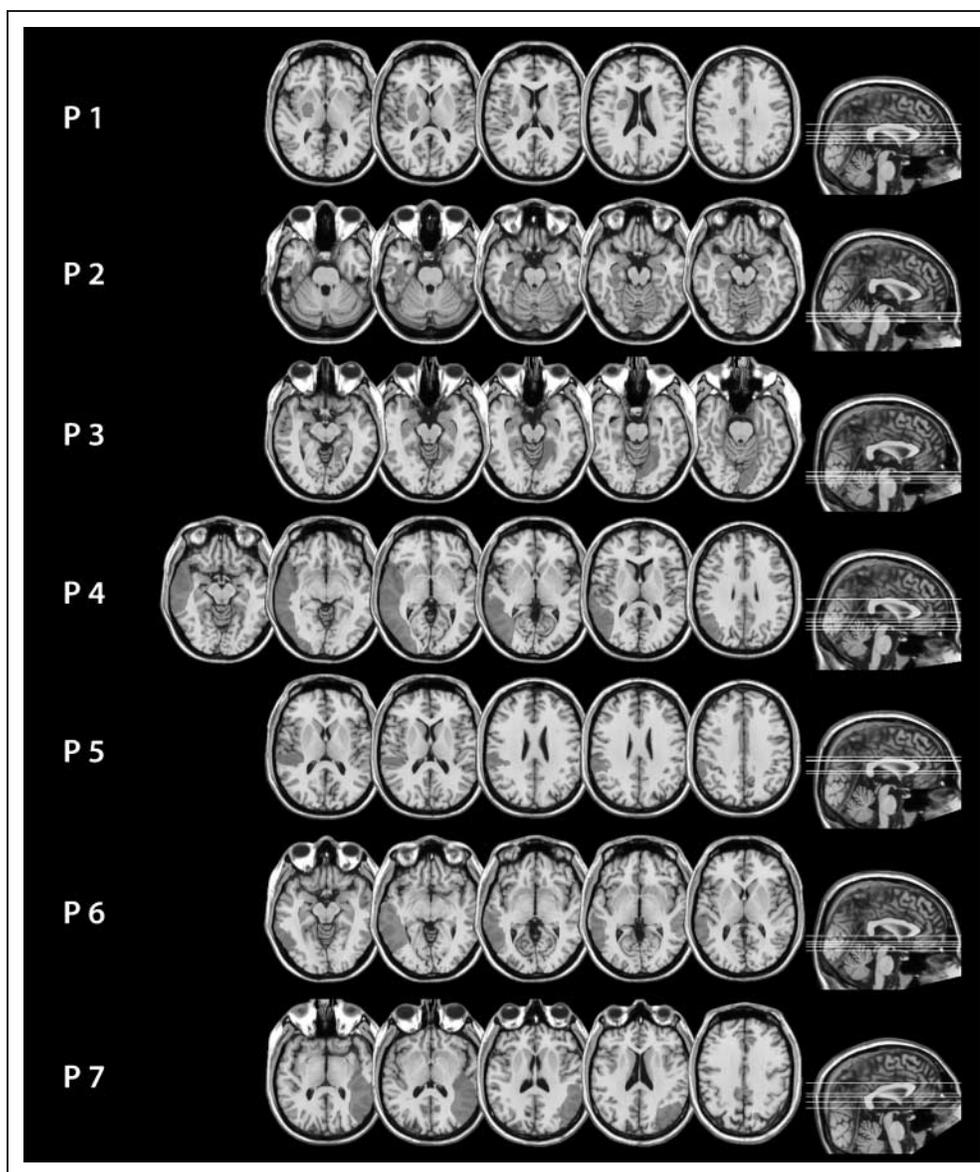


Figure 1. H+ patients. Lesion reconstruction images from MRI, reported onto the normalized MNI template (www.bic.mni.mcgill.ca/cgi/icbm_view).

Figure 2. H− patients. Lesion reconstruction images from MRI, reported onto the normalized MNI template (www.bic.mni.mcgill.ca/cgi/icbm_view).



point-light animations of arm gestures and they were requested to verbally name the type of action performed in each point-light movie. Each trial began with the presentation of a black screen containing a central white fixation point for 500 msec. Next, a randomly selected, 5-sec movie depicting a point-light action was presented. Then, the screen reverted to black until the experimenter initiated the next movie following the subject's response. Each movie subtended approximately between 12° and 15° of visual angle from the observer's position relative to the display monitor. Before the task, observers completed a block of 10 practice trials to familiarize themselves with the apparatus and the task. Minimal feedback was given during the practice trials, whereas no feedback was given during experimental trials.

One block of trials was administered for each of three possible stimulus orientation conditions (Real-MC, Flip-MC, and I-RMC or I-FMC). Block order was counterbalanced

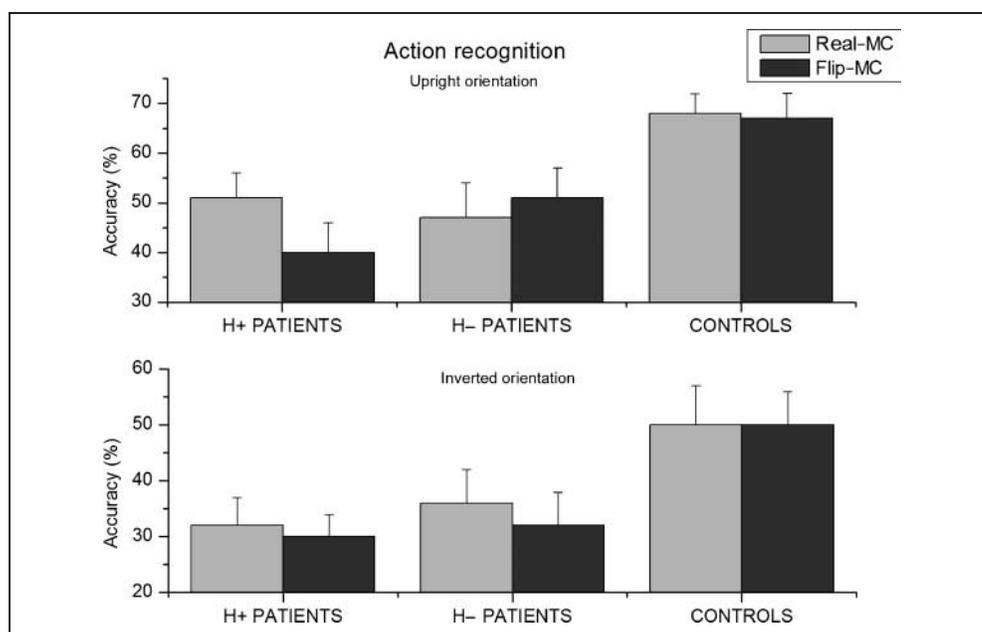
across subjects. Each block contained 90 movie trials: 10 types of actions × 3 versions of each action × 3 different actors (the observer and two other participants for H+ patients and healthy controls, and two other participants for H− patients). To avoid any confounding effects from the movement differences between patients and healthy participants, patients saw only movies of actions performed by patients, whereas controls saw only actions performed by healthy subjects. For H− patients, the same database of movies assembled for H+ patients was used.

Results

Action Recognition

The primary comparison of interest concerned action recognition performance by H+ patients when actions were depicted as originally performed (Real-MC) and as

Figure 4. Performance accuracy in the action recognition experiment by H+ patients, H- patients, and controls. Real-MC and Flip-MC movement conditions. The upper part shows result for upright movies, and the lower part shows results for inverted movies.



in controls (68%) than in hemiplegic patients (46%), and in Real-MC (59%) than in Flip-MC (55%). This effect depended on the significant difference found in patients between action recognition in the Real-MC (52%) and in the Flip-MC (41%; $p < .0004$); this difference was not found in controls: Real-MC = 68%; Flip-MC = 67% ($p = .58$).

More interestingly, the two-way interaction Agent \times Group was also significant [$F(1, 18) = 4.74, p < .05$]. That is, mean action recognition accuracy was higher when patients viewed self-produced actions (53%) than when they viewed actions produced by other patients (47%; $p < .02$). The performance by healthy controls did not vary when they viewed self-produced actions (67%) and actions produced by other subjects (68%).

Discussion

The goal of this psychophysical experiment was to determine whether motor system impairment compromises visual sensitivity to human action. Three main findings were obtained. First, brain-damaged patients both with and without hemiplegia were found to be impaired in their ability to recognize point-light displays of arm movements in comparison to healthy controls. Second, only in patients selected for a motor deficit in their contralesional upper limb were action recognition abilities especially compromised when observed arm movements corresponded to their hemiplegic arm. Third, viewing self-produced actions enhanced action recognition in hemiplegic patients.

This pattern of results is consistent with the hypothesis that the perceptual analysis of action is compromised when observers cannot remap an observed action onto their damaged contralesional hemisoma. This deficit cannot be explained by a generic decrement in cognitive resources as

a result of brain damage because only brain-damaged patients with hemiplegia, but not brain-damaged patients without hemiplegia, showed a different performance in recognizing actions executed with either arm.

Another possible explanation for the previous findings might be that hemiplegic patients suffered a generic deficit in visual processing of biological motion, irrespectively from any motor impairment. In other words, their action recognition deficit could be due not to a failure in the action simulation mechanism but to an impairment in motion processing. Brain-damaged patients, indeed, can be impaired in processing biological motion, irrespectively of any motor impairment (Saygin, 2007; Vaina & Gross, 2004; Battelli, Cavanagh, & Thornton, 2003). This hypothesis, although unlikely (i.e., it cannot account for the critical laterality effects found with hemiplegic observers), was further investigated by the following experiment.

EXPERIMENT 2: RECOGNITION OF POINT-LIGHT ANIMALS

Previous research has shown that typical observers can recognize point-light depictions of nonhuman animals (Bellefeuille & Faubert, 1998; Mather & West, 1993). Yet, the visual perception of animal motion involves neural processes that diverge from those underlying the perception of human motion. For example, when a human observer views a fully rendered movie of a barking dog, fMRI data indicate that the observer's action simulation mechanisms are not engaged (Buccino et al., 2004). Similarly, EEG data suggest that action simulation mechanisms are activated during the visual perception of human motion, but not animal motion, in observers as young as 5 years old (Martineau & Cochin, 2003). In sum, the visual perception

of point-light displays of animal motion appears to depend upon the same high-level visual and cognitive processes involved in the perception of point-light displays of human motion, but not on the action simulation mechanisms triggered during human action perception. Therefore, assessment of visual sensitivity to animal motion provides a means of controlling for the roles of high-level visual and cognitive processes in the results of Experiment 1.

In the following control experiment, H+ patients, H- patients, and controls observed point-light movies of animals in motion and attempted to identify each animal. This animal recognition task was designed to require the same visual and cognitive processing of complex, biological motion as the human action recognition task, without tapping the motor simulation mechanism involved in human motion perception. Thus, the goal of this experiment was to determine whether generic deficits in high-level visual and cognitive processes resulting from the brain damage experienced by the hemiplegic observers could account for the key result of Experiment 1, specifically, that hemiplegic observers show decreased visual sensitivity to human actions involving a limb that corresponds to the observer's hemiplegic limb. Simulation-based theories of action perception would predict that generic deficits in visual motion perception and/or cognitive recognition process might account for overall performance differences between patients and controls, *but should not account* for the laterality-specific deficit found in hemiplegic observers when they viewed actions corresponding to the hemiplegic side of their body.

Methods

Participants

The same subjects in Experiment 1 participated in Experiment 2. Experiment 2 was conducted in a different experimental session from that of Experiment 1.

Stimuli

The stimuli consisted of point-light movies of naturally moving animals. These stimuli were created by systematically positioning white points on the major joints and head of each animal, on a frame-by-frame basis, depicted in a digital videotape. Following this, everything was removed from each frame except the white points that appeared against a homogenous black background. Number of points varied for different animals. From the observer's viewing position, each movie subtended between 12° and 15° of visual angle. Each point-light movie was cut to a fixed stimulus duration of 5 sec.

Across movies, the actions of a dog, monkey, chicken, snake, and bird were individually depicted. Each animal's action was always natural and common for that animal. Thus, the chicken was seen walking across a barnyard and pecking the ground for food. The monkey was seen

walking on the ground and climbing a tree. The bird flew in the sky, the snake slithered along the ground, and so forth. Across the different movies, animals' actions unfolded in different directions and were depicted from different perspectives. Each of the five animals was shown in four different movies for a total of 20 movies.

Experimental Design and Procedure

The animal recognition task lasted about 30 min. The experimental setup was the same as in Experiment 1. Observers were told that they would see some briefly presented point-light movies consisting of different animals performing movements typical of their species. The observer's task was to view each movie and to name the animal depicted in it. There was no time limit to respond, but participants were instructed to wait until each movie ended before responding. The same 20 different movies were displayed to each participant in random order. Before the task, each observer completed a block of 10 practice trials with movies that differed from those of the experimental trials. Feedback was provided during the practice trials but not during the experimental trials.

Results

The percentage of correctly identified animals across the 20 trials was compared between H+ patients, H- patients, and controls by means of one-way ANOVA with group as a between-subjects factor. The main effect of group was significant [$F(2, 25) = 4.13, p < .03$] and Newman-Keuls post hoc comparisons showed that performance accuracy was higher in control observers (65%) in comparison to both H+ patients (39%; $p < .03$) and H- patients (44%; $p < .04$); the two groups of patients did not differ from each other ($p = .58$). Thus, brain damage appears to decrease performance in the recognition of biological motion presented as point-light displays.

To determine whether the generic processing deficit found in this experiment could explain the laterality specific deficit of H+ patients found in Experiment 1, performance from Experiment 1 was reanalyzed by taking into account the performance from Experiment 2. To that end, an ANCOVA was performed on the results from Experiment 1 with group (H+, H- patients and controls) as the between-subjects factor, movement condition (Real-MC vs. Flip-MC) and orientation (upright and inverted movies) as the within-subjects factors, and the accuracy in animal recognition task as a continuous regressor. The effect of the regressor was significant [$F(1, 24) = 5.05, p < .04$], supporting the view that human action recognition and animal recognition share some common processes (Buccino et al., 2004; Martineau & Cochin, 2003). Interestingly, when the performance in the human action recognition task (Experiment 1) was corrected for the performance in the animal recognition

task (Experiment 2), the main effect of group was no longer significant [$F(2, 24) = 1.64, p = .21$]. Specifically, mean corrected accuracy was 40% in H+ patients, 44% in H- patients, and 54% in healthy controls. However, and crucially for the aim of this study, the two-way interaction Group \times Movement was still significant [$F(2, 24) = 8.2, p < .003$]. That is, correct mean accuracy for hemiplegic observers in Experiment 1 was higher when they viewed Real-MC in upright orientation, in which they viewed arm gestures corresponded to their unaffected arm (54%), than when they viewed Flip-MC (41%), in which they viewed arm gestures that corresponded to their paralyzed arm. Conversely, H- patients and control observers demonstrated equal visual sensitivity to the originally oriented and the mirror-reversed point-light displays of arm motion (correct mean accuracy: H- patients = 49% and 53%; controls = 60% and 63%; in Real-MC and Flip-MC in upright orientation, respectively). Correct mean accuracy in inverted orientation for Real-MC and Flip-MC, respectively, was 33% and 31% in H+ patients, 38% and 36% in H- patients, and 45% and 46% in healthy controls.

Finally, accuracy in the animal recognition task was used also to control for the effect of visual processing abilities on action recognition of self-produced and other-produced movements. To this aim, H+ patients' and controls' performance in the action recognition task was compared across trials that depicted self-produced actions and trials depicting the other-produced actions, taking into account the performance in the animal recognition task. An ANCOVA was conducted with the within-subjects factors of movement condition (Real-MC vs. Flip-MC) and agent (self-produced actions vs. other-produced actions), the between-subjects factor of group (H+ patients and controls) and the accuracy in the animal recognition task as a covariate.

The effect of the regressor was significant [$F(17, 1) = 19.52, p < .0001$]. The two-way interaction Agent \times Group was also significant [$F(1, 17) = 12.79, p < .003$], showing that, when corrected for visual processing abilities, action recognition in hemiplegic patients was higher when viewing self-produced movements (52%) rather than other-produced movements (46%). Such difference was not found in controls (64% and 64%). Thus, the difference between H+ patients and controls in visual processing abilities could not account for the better sensitivity in recognizing self-produced actions found in hemiplegic observers.

GENERAL DISCUSSION

The results of two psychophysical studies clearly suggest that a lesion of the motor system affects action comprehension. To demonstrate a specific role of motor impairment in action recognition, hemiplegic (H+) patients viewed and attempted to name movements that appeared to have been performed with either the arm on their

hemiplegic side (Flip-MC) or with the arm on their unaffected side (Real-MC). Their performance was compared to that by a group of brain-damaged patients without any impairment at the motor system (H- patients) and by healthy controls. Action recognition in patients with or without motor deficits was worse than in healthy controls. However, although H- patients and control observers demonstrated no difference in their ability to recognize actions performed with an upper limb from either side of a human body, hemiplegic observers were better able to recognize actions that appeared to have been performed with an upper limb that corresponded to the unaffected side than to the hemiplegic side of their body. This laterality effect suggests a strong link between action recognition and motor impairment that is difficult to dismiss as the result of a generic impairment of cognitive resources. Such impairment may explain the general performance difference between patients and controls, but cannot explain the difference in action recognition for actions performed with the contralesional and the ipsilesional side of the body found only in hemiplegic patients. A generic cognitive impairment should indeed impact a hemiplegic observer's ability to recognize actions performed with either arm or alternatively should produce the same pattern of results in hemiplegic and in nonhemiplegic patients.

Furthermore, to ensure that laterality-specific deficits in action perception did not result from high-order disorders of global analyses of complex visual motion, but was specifically due to hemiplegic observers' motor deficits, participants were also tested in another biological motion processing task; namely, the recognition of animals in point-light displays. Although the animal recognition task required the same high-level visual processing as the human action recognition task, it should not have triggered motor simulation mechanisms (e.g., Martineau & Cochin, 2003). Simply put, human observers cannot simulate bird flight or chicken pecks or snake slithers because those actions are not part of a human observer's own motor repertoire (Buccino et al., 2004). The results of Experiment 2 identified significant performance impairments by patients relative to control observers, suggesting that the brain lesions of hemiplegic and nonhemiplegic observers affected generic high-level visual and/or cognitive processing. However, regression analyses also indicate that such generic deficit(s) per se cannot account for the lateralized action recognition impairments exhibited by the hemiplegic observers. Only hemiplegic observers showed significantly different levels of visual sensitivity to actions from either side of the body. Across the patients and control observers, this laterality in perceptual sensitivity matched the laterality in action execution ability. That is, laterality-dependent deficits in perceptual sensitivity occurred when hemiplegic observers viewed actions that they either could or could not perform. Thus, whereas the perception of human and animal movement relies on some common visual processes, action understanding further requires the involvement of the motor system, which is impaired

in hemiplegic patients and not in nonhemiplegic patients nor in healthy controls.

Numerous researchers have suggested that during action observation, observers implicitly and automatically activate an internal representation, or an implicit simulation, of the motor program needed to plan the observed action. In this way, the observed action is thought to be remapped onto the observer's own body and, as a result, the observer can link an observed action to his or her own motor repertoire, or action vocabulary (e.g., Rizzolatti, Fogassi, & Gallese, 2002), and in so doing, can recognize the viewed action. The current results suggest that this simulation mechanism is asymmetrically affected in hemiplegic observers. Hemiplegia involves brain damage to one hemisphere of the motor system affecting the contralesional side of the body, and spares the motor system in the other hemisphere and the ipsilesional side of the body. As a result, when observers with hemiplegia view actions performed with the hand contralateral to their brain lesion, they are unable to correctly map the observed hand action onto their own body. In this way, hemiplegic observers can neither access the correct motor representation of an observed action, nor use the somatosensory and proprioceptive feedback associated to the representation of that action (Wolpert, Doya, & Kawato, 2003). As a result, action perception is impaired.

Other recent studies have related impairments at the motor system with action perception deficits. In particular, Pazzaglia, Pizzamiglio, et al. (2008) and Pazzaglia, Smania, et al. (2008) have recently shown that patients with apraxia are also impaired in recognizing the correct execution of gestures. Apraxia is a deficit of motor planning, involving high level of motor processing. The results of the present study suggest that even low-level impairments in action execution are specifically associated to a deficit in action recognition, suggesting that the remapping of visual information about actions onto the motor simulation mechanism involves basic motor system processes.

Another important aspect of the design of the current research is the use of point-light animations rather than fully rendered movies. This method ensured that action recognition performance did not depend upon high-level cognitive or contextual cues. Moreover, this method also allowed for further support of simulation theory. Previous researches have shown that inversion along the vertical axes disrupts the visual analysis of point-light defined actions (e.g., Blake & Shiffrar, 2007; Sumi, 1984), as observers are unable to map these percepts onto their body. Consistent with this, when hemiplegic and control observers viewed actions that they could not perform, either because those actions corresponded to the hemiplegic side of their body and/or because those actions were inverted, their performance in the action recognition task dropped significantly.

Another aim of this work was to examine whether visuomotor remapping of observed actions was influenced by the identity of the agent, and in particular, whether view-

ing self-generated actions induced a stronger visuomotor remapping. To that end, we analyzed the action recognition results from Experiment 1 as a function of whether the observer viewed self-generated or other-generated actions. Action recognition performance was modulated by actor identity. That is, hemiplegic observers were more accurate in naming point-light defined actions when they saw actions that they had performed. This effect was not found in control observers. However, in healthy observers, action recognition was much better than in brain-damaged patients. Thus, a fully intact simulation mechanism might have been sufficient to support action recognition, without benefiting from any supplementary effects due to actor identity.

The effect of self-produced movements on action recognition is new. Previous studies showed that healthy subjects are specially tuned to visually processing their own movements (Daprati et al., 2007a, 2007b; Loula et al., 2005) or movements they have learned to perform (Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2005, 2006; Casile & Giese, 2006). Here we show that this special tuning for self-related movements facilitates the access to the representation of a visually presented action. This effect might depend on relatively elaborated simulation during the perception of self-produced actions because such visual information provides the optimal match for sensory-motor representation in the observer's motor system. The current results indicate that this effect is especially evident in a damaged system.

In summary, the current research shows for the first time that an elementary lesion to the motor system systematically impairs action perception by interfering with the visuomotor remapping of an observed action onto the observer's body. Furthermore, observation of self-generated movements appears to have a modulatory effect on this form of visuomotor resonance.

Acknowledgments

We thank Silvia Bonifazi for her help in patient selection, Sapna Prasad for her help in stimuli editing, Sabrina Stanziani and Claudia Biondi for their help in lesions drawing, and Elisa Magnini for her help in figures drawing.

Reprint requests should be sent to Andrea Serino, Centro studi e ricerche in Neuroscienze Cognitive, Università di Bologna, Via Brusi, 20; 47123 Cesena, Italy, or via e-mail: andrea.serino@unibo.it.

REFERENCES

- Battelli, L., Cavanagh, P., & Thornton, I. M. (2003). Perception of biological motion in parietal patients. *Neuropsychologia*, *41*, 1808–1816.
- Bellefeuille, A., & Faubert, J. (1998). Independence of contour and biological-motion cues for motion-defined animal shapes. *Perception*, *27*, 225–235.
- Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, *58*, 47–73.

- Bosbach, S., Cole, J., Prinz, W., & Knoblich, G. (2005). Inferring another's expectation from action: The role of peripheral sensation. *Nature Neuroscience*, *8*, 1295–1297.
- Buccino, G., Lui, F., Vanessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004). Neural circuits involved in the recognition of actions performed by nonconspicuous: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.
- Buxbaum, L. J., Kyle, K. M., & Menon, R. (2005). On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. *Brain Research, Cognitive Brain Research*, *25*, 226–239.
- Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*, 1243–1249.
- Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, *16*, 1905–1910.
- Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology*, *16*, 69–74.
- Collin, C., & Wade, D. (1990). Assessing motor impairment after stroke: A pilot reliability study. *Journal of Neurology, Neurosurgery, and Psychiatry*, *53*, 576–579.
- Daprati, E., Wriessnegger, S., & Lacquaniti, F. (2007a). Kinematic cues and recognition of self-generated actions. *Experimental Brain Research*, *177*, 31–44.
- Daprati, E., Wriessnegger, S., & Lacquaniti, F. (2007b). Knowledge of one's kinematics improves perceptual discrimination. *Consciousness and Cognition*, *16*, 178–188.
- De Renzi, E., Motti, F., & Nichelli, P. (1980). Imitating gestures: A quantitative approach to ideomotor apraxia. *Archives of Neurology*, *37*, 6–10.
- Duvernoy, O., Malm, T., Thuomas, K. A., Larsson, S. G., & Hansson, H. E. (1991). CT and MR evaluation of pericardial and retrosternal adhesions after cardiac surgery. *Journal of Computer Assisted Tomography*, *15*, 555–560.
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, *12*, 189–198.
- Funk, M., Shiffrar, M., & Brugger, P. (2005). Hand movement observation by individuals born without hands: Phantom limb experience constrains visual limb perception. *Experimental Brain Research*, *164*, 341–346.
- Gallese, V. (2007). Before and below "theory of mind": Embodied simulation and the neural correlates of social cognition. *Philosophical Transactions Royal Society of London, Series B, Biological Sciences*, *362*, 659–669.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, *2*, 493–501.
- Gauthier, L., Dehaut, F., & Joanette, Y. (1989). The Bells test: A quantitative and qualitative test for visual neglect. *International Journal of Clinical Neuropsychology*, *11*, 49–54.
- Hamilton, A., Wolpert, D., & Frith, U. (2004). Your own action influences how you perceive another person's action. *Current Biology*, *14*, 493–498.
- Iacoboni, M., & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews Neuroscience*, *7*, 942–951.
- Jacobs, A., & Shiffrar, M. (2005). Walking perception by walking observers. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 157–169.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, *14*, 201–211.
- Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 210–220.
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology (Paris)*, *102*, 59–70.
- Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, *58*, 25–45.
- Martineau, J., & Cochin, S. (2003). Visual perception in children: Human, animal and virtual movement activates different cortical areas. *International Journal of Psychophysiology*, *51*, 37–44.
- Mather, G., & West, S. (1993). Recognition of animal locomotion from dynamic point-light displays. *Perception*, *22*, 759–766.
- Pavlova, M., Staudt, M., Sokolov, A., Birbaumer, N., & Krageloh-Mann, I. (2003). Perception and production of biological movement in patients with early periventricular brain lesions. *Brain*, *126*, 692–701.
- Pazzaglia, M., Pizzamiglio, L., Pes, E., & Aglioti, S. M. (2008). The sound of actions in apraxia. *Current Biology*, *18*, 1766–1772.
- Pazzaglia, M., Smania, N., Corato, E., & Aglioti, S. M. (2008). Neural underpinnings of gesture discrimination in patients with limb apraxia. *Journal of Neuroscience*, *28*, 3030–3041.
- Reed, C. L., & Farah, M. J. (1995). The psychological reality of the body schema: A test with normal participants. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 334–343.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2002). Motor and cognitive functions of the ventral premotor cortex. *Current Opinion in Neurobiology*, *12*, 149–154.
- Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioural Neurology*, *12*, 191–200.
- Saygin, A. P. (2007). Superior temporal and premotor brain areas necessary for biological motion perception. *Brain*, *130*, 2452–2461.
- Saygin, A. P., Wilson, S. M., Hagler, D. J., Jr., Bates, E., & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *Journal of Neuroscience*, *24*, 6181–6188.
- Schutz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Sciences*, *11*, 349–355.
- Sumi, S. (1984). Upside-down presentation of the Johansson moving light-spot pattern. *Perception*, *13*, 283–286.
- Troje, N. F., Westhoff, C., & Lavrov, M. (2005). Person identification from biological motion: Effects of structural and kinematic cues. *Perception & Psychophysics*, *67*, 667–675.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al. (2002). Automated anatomical labeling of activations in

