



## Cortical Modulation of Whole Body Movements in Brain-Damaged Patients

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### ABSTRACT

The aim of the present study was to assess whether the consistent bias in reproducing distances and lengths on visual tasks that characterizes hemispatial neglect is also present when whole body displacements have to be calculated and reproduced. Two different experiments were proposed to participants with right brain lesions and neglect syndrome (RN+), right (RN–) and left brain lesions (LN–) without neglect and to participants without brain damage (C). In Experiment 1, participants actively reproduced passive linear displacements in the same or in a different direction. This task could be performed using only vestibular and somatosensory input, since no relevant visual input was available. In Experiment 2, relevant visual information had to be integrated with vestibular and somatosensory information in order to make the active reproduction.

In Experiment 1, all brain-damaged groups reproduced the horizontal displacements similarly to the control group and without any spatial asymmetry. In Experiment 2, when vestibular, somatosensory and visually remembered information was required to produce an integrated mental representation, RN+ processed contralesional displacements differently from ipsilesional ones.

Rectilinear displacements of the whole body in space were not affected by focal left and right brain lesions, suggesting that the computation of nonvisual information can be accomplished by brain structures different from those involved in spatial visual processes. However, when body displacements in space required a mental representation based on visual and nonvisual sensory information, a significant asymmetry appeared only in patients with hemispatial neglect. Some attempts are made to identify the neural substrates involved in this integration.

### INTRODUCTION

In mammals, navigation requires the adequate perception, reconstruction, memorization and retrieval of angular and linear motion of the body in space by the brain. This paper concerns the problem of perception and memory of translations.

Studies on normal individuals have shown that it is possible to accurately reproduce a whole-body displacement in space by integrating convergent visual, vestibular and somatosensory inputs and efferent copies of motor commands

(Berthoz, Israel, George-Francois, Grasso, & Tsuzuku, 1995; Israël, Chapuis, Glasauer, Charade, & Berthoz, 1993; Ivanenko, Grasso, Israël, & Berthoz, 1997). Berthoz et al., suggested that “the brain stores the dynamic properties of the whole passive linear motion” and may reproduce the distance of the displacement by reproducing the velocity profile derived from vestibular inputs, complemented by somatosensory cues.

Although it has been suggested that the “vestibular cortex” contributes to body turns (Bottini et al., 1994; Brandt, Dieterich, & Danek,

1994; Grüsser, Pause, & Schreiter, 1990; Lobel, Kleine, Le Bihan, Leroy-Willig, & Berthoz, 1998), very little is actually known about the neural structures responsible for this integration in the case of linear displacement.

One way to clarify this issue is to study patients with focal brain lesions while they perform tasks requiring multisensory integration. Within this classical anatomo-clinical correlation approach, special attention is also given to hemispatial neglect. The critical features of this disorder are clearly characterized by an asymmetrical processing of space. The inclusion of a subgroup of hemispatial neglect patients contributes to the understanding of the neural mechanisms underlying the processing of body motion in space and the role of vestibular and other nonvisual information in sustaining hemispatial disorders.

It has been shown that right brain-damaged patients with contralesional neglect have consistent biases (i.e., a horizontal anisometry; Bisiach, Rusconi, Peretti, & Vallar, 1994; Bisiach, Pizzamiglio, Nico, & Antonucci, 1996) in reproducing distances in purely visual tasks. When neglect patients try to duplicate the length of a horizontal line by drawing an identical line to the left or to the right of a given stimulus, they systematically tend to increase the length on the left (contralesional) side but not on the right side (Chokron, Bernard, & Imbert, 1997). Similarly, when they are given two points and asked to draw a third point exactly the same distance to the left and to the right of the original stimulus, these patients overextend the endpoint toward the left side and undershoot it on the right side (Bisiach et al., 1996).

Since neglect is a supramodal deficit, and is not just confined to visual perception, and since it is a deficit of whole space representation, it most likely affects any kind of spatial task. Performing whole-body displacements in space mostly requires processing vestibular and somatosensory inputs in the vestibular nuclei of the brain stem, in the thalamus, and in other cortical areas (Grüsser, Guldin, Harris, Lefebvre, & Pause, 1992). In normal subjects, no evidence of asymmetrical brain representation in processing this information has been reported (Grüsser et al., 1992; Lobel

et al., 1998). Therefore, any asymmetry detected when the neglect patient performs whole-body displacements basing space estimation on vestibular and somatosensory inputs should be attributed to a top-down influence of the parietal systems processing egocentric space representation. On the other hand, the absence of asymmetries supports the hypothesis that neglect does not affect vestibular and somatosensory processes, and that this may be accomplished entirely by subcortical structures and by nonparietal cortical areas. If this is true, it can be hypothesized that neglect affects whole-body space displacements only if vestibular and somatosensory information has to be integrated with visual inputs in a more complex egocentric framework representation of space. In the first experiment, we tested this hypothesis by administering whole-body displacement tasks to neglect patients. It was possible to perform these tasks only by processing vestibular and somatosensory information. In a second experiment (Exp. 2), we studied the same neglect patients while they performed a task in which vestibular and somatosensory information was combined with relevant visual information to produce an integrated mental representation of space.

## EXPERIMENT 1

In the first experiment, we investigated the distance replication of linear whole-body displacements using a specially designed robot (cart). The participants could replicate a passively imposed whole-body displacement by actively moving the robot in the same direction (leftward-leftward, rightward-rightward and forward-forward) or in a different direction (i.e., leftward-forward; forward-rightward, etc.; see Fig. 1).

These different conditions allowed us to evaluate whether the patients were able to use "vestibular memory" when they had to reproduce the passive displacement in the same direction and generate a representation of the distance when they had to reproduce the displacement in a different direction. Moving in a different direction, the vestibular and somatosensory information changed completely. In order to replicate the

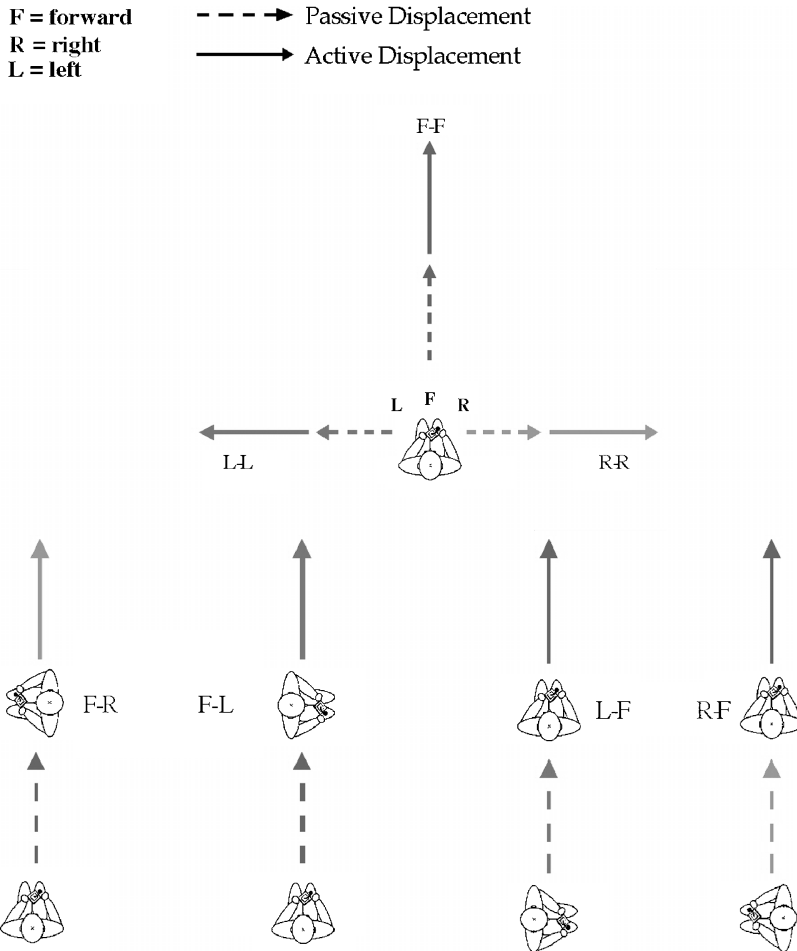


Fig. 1. Distance replication in the same direction: left-left (L-L), right-right (R-R) and forward-forward (F-F). Distance replication in different directions: forward-right (F-R), forward-left (F-L), left-forward (L-F) and right-forward (R-F). In each condition, the first letter refers to passive displacement (dotted line) and the second letter to active displacement (solid line).

same distance, the passive spatial displacement had to be computed by using some parameters (i.e., velocity profile, time, etc.) to compare the initial, passive reference displacement with a successive active displacement based on a different set of sensory information.

A pilot experiment was carried out to determine whether patients affected by severe neurological impairments would be able to participate. In this study, both controls and right brain-damaged patients were seated on the robot. After a passive linear displacement of variable length (2, 3, and 4 m), the patients were asked to actively

move the robot to reproduce the same distance in the same direction. Two conditions were used: (a) no vision (patients were blindfolded); (b) free vision. There were no significant differences between the two conditions, that is, there was no difference in accuracy in reproducing different lengths in the free and no vision conditions in either brain-damaged patients or normal controls.

However, the long duration (about 3 hr) of the experiment and increasing fatigue of the subjects indicated the need to reduce the number of trials. Since some patients and controls reported slight motion sickness in the blindfolded condition, and

since no differences were detected between the two vision conditions, we decided to present the task in free vision. To further reduce the number of trials, we also decided to use only the 3-m length for this experiment.

Care was taken to eliminate visual cues from the experimental environment: all objects were removed from the room; the walls, the door and the windows were completely covered by blue curtains; the floor and the ceiling were painted blue; a dim central light was used.

Special attention was also given to the duration of the stimuli. Neglect patients can be affected by a distorted perception of time in the neglected side of the space. In fact, Basso, Nichelli, Frassinetti, and Di Pellegrino (1996) found that a patient with left unilateral neglect overestimated the visual stimuli presented in the neglected space. Here, to discourage using time as a way of responding to the task, we introduced a high proportion of catch trials in which the time of the passive translation was shorter or longer than the experimental trials. Moreover, in a different experiment we used visual stimuli to investigate the ability of all experimental groups to estimate time.

## MATERIALS AND METHODS

### Subjects

Four groups of 5 participants each were studied: (a) right brain-damaged patients with neglect (RN+) and (b) without neglect (RN-), (c) left brain-damaged patients without neglect (LN-) and (d) normal controls (C) of comparable age (ANOVA:  $F = 0.296$ ; *ns*) and education (ANOVA:  $F = 1.44$ ; *ns*). All patients suffered from unilateral lesions deriving from a unique CVA; time from onset did not differ (ANOVA:  $F = 1.667$ ; *ns*). No patients showed symptoms of previous psychiatric disorders or signs of dementia. None of the brain-damaged patients showed signs of visual field defects evaluated by Goldman perimeter.

An extensive standard neuropsychological assessment (Spinnler & Tognoni, 1987) was made to evaluate the presence of cognitive deficits. All the LN- patients were affected by aphasia; however, they were able to fully understand the instructions. None of the patients showed signs of cognitive decay or memory deficits. An ANOVA revealed no between-group differences in level of general cognitive functioning, measured by Raven's Progressive Matrices ( $F = 1.431$ ; *ns*); also, no between-group differences were found in Digit span

( $F = 0.687$ ; *ns*), Corsi span ( $F = 0.111$ ; *ns*) or Episodic memory ( $F = 1.855$ ; *ns*).

Neglect was assessed using a standardized battery that included the Line Cancellation task (Albert, 1973), the Letter Cancellation task (Diller & Weinberg, 1977), the Wundt-Jastrow Area Illusion test (Massironi, Antonucci, Pizzamiglio, Vitale, & Zoccolotti, 1988) and the Sentence Reading test (Pizzamiglio et al., 1992). Subjects were included in the neglect group when they performed at a pathological level on at least two of the four tests.

All participants gave their informed consent to participate in the study, which was approved by the local ethical committee. Patients' demographic and clinical data are shown in Table 1.

### Stimuli

#### Linear Displacement

For this experiment, we used the "Otomac" mobile robot (Megaris<sup>TM</sup>, Caserta, Italy), equipped with a rotating seat and controlled by an on-board PC. The PC makes it possible to program acceleration and distance of "passive" displacements. A pressure-sensitive spring button can also operate the robot in "active" displacements (i.e., guided by the participants); in this case, speed is directly proportional to button pressure. The PC records distances, accelerations, and time of the active displacements, reflecting the motion the robot produces as a result of the control inputs. It also makes possible the graphic representation of the mean velocity profile for each displacement condition.

During the experimental trials, the participants were first passively and linearly displaced 3 m in one of the three different directions, that is, leftward, forward, or rightward. Then they were required to replicate the same distance in the same or in a different direction by operating the pressure-sensitive spring button (see Fig. 1). The participants were not asked to reproduce velocity profiles or peak velocities.

During the passive displacement, the velocity profile was triangular, the magnitude of the acceleration/deceleration was constant ( $0.18 \text{ m/s}^2$ ), and the peak velocity was 0.65 m/s. The training and the experiment were performed in one session in a 6 m × 9 m room.

#### Time Estimation

The subject was seated at a distance of 57 cm from a 21-in. screen controlled by an Apple Macintosh computer with SuperLab software (Cedrus Corporation, USA); the patient's body midline was aligned with the center of the screen. In each trial, a visual (reference) stimulus (a 100 cm<sup>2</sup> white square in the center of a dark background screen) was presented for 6, 8 or 10 s followed by a 10-s delay and a probe stimulus (the same white square).

Table 1. Demographic and Clinical Data of Left (LN-) and Right Brain Damaged Patients With (RN+) and Without (RN-) Neglect.

Case	Group	Sex	Age	Months from onset	Lesion site <sup>a</sup>	Line Cancellation <sup>b</sup>		Letter Cancellation <sup>c</sup>		Sentence Reading <sup>d</sup>	Wundt Jastrow <sup>e</sup>		Personal Neglect <sup>f</sup>
						Left	Right	Left	Right		Left	Right	
						1	RN+	M	71	10	Caudate N.; pvWM	11	
2	RN+	F	51	2	6, 4, 3-1-2, 41, 42, 44, 45, 18, 19, 39, 40, 5, 7	10	10	13	48	6	20	20	0
3	RN+	M	68	7	22, 21, 44, 45, 20, 41, 42, 18, 19, 6, 4, 3-1-2, 40, 39	11	10	37	50	3	14	20	7
4	RN+	M	47	2	21, 37, 28, 36, 22, 20, 44, 45, 41, 42, 40, 39	11	10	23	34	2	18	20	2
5	RN+	M	70	3	44, 45, 6, 4, 3-1-2, 40, pvWM	10	10	24	44	6	20	20	0
6	RN+	F	55	3	*	11	10	47	51	6	16	20	3
7	RN+	F	67	5	*	10	10	35	49	6	18	20	4
8	RN-	M	65	2	Th, caudate N.	11	10	52	51	6	20	20	0
9	RN-	M	73	3	Posterior Th, perinsular WM	11	10	52	49	6	20	20	0
10	RN-	M	60	1	Internal capsule	11	10	53	51	6	20	20	0
11	RN-	M	70	1	Internal capsule, basal ganglia, lenticular N., corona radiata	11	10	52	51	6	20	20	0
12	RN-	M	57	1	Lenticular N., internal capsule, frontal corona radiata	11	10	53	51	6	20	20	1
13	LN-	M	76	4	3-1-2, 7, 22, 39, 40, 41, 42, 44	11	10	53	51	*	20	20	0
14	LN-	M	65	3	39, 40	11	10	53	51	*	20	20	0
15	LN-	M	60	1	38	11	10	53	51	*	20	20	0
16	LN-	M	55	11	*	11	10	52	51	*	20	20	0
17	LN-	M	50	48	*	11	10	53	51	*	20	20	0

<sup>a</sup>Broadman's areas of cortical lesions and a description of the structures involved in the subcortical lesions. N. = nucleus; pvWM = periventricular white matter; Th = thalamus; \* = data not available.

<sup>b</sup>Number of marked items in left (max. 11) and right (10) hemispaces.

<sup>c</sup>Number of crossed-out target-letters in left (max. 53) and right (max. 51) hemispaces.

<sup>d</sup>Number of correct responses (max. 6).

<sup>e</sup>Number of perceived leftward (max. 20) and rightward (max. 20) illusions.

<sup>f</sup>Severity score (max. 9). LN-: The sentence reading test was not performed due to the presence of aphasic disorders.

## Procedure

### Linear Displacement

The subject was seated on the robot and secured by two safety belts; his/her head was restrained by a cushioned support to prevent rotations. During the displacements, the subject wore headphones delivering white noise.

Before starting the experimental procedure, the participants were trained for at least 10 min (until each participant felt safe and comfortable) to be passively displaced and to actively move the robot by pressing the button.

Three blocks of trials required reproducing the distance in the "same" direction as the passive displacement (left-left, right-right, forward-forward); four blocks required reproducing the distance in a "different" direction (forward-right, forward-left, right-forward, left-forward).

In the "same" condition, the participant was seated on the robot and was passively moved in one of the three directions. Then, the robot was stopped for 10 s, and immediately afterward the participant guided the robot to actively reproduce the passive transportation.

In the "different" condition, shown in Figure 1, the participant was seated on the robot and was passively moved in one direction; then, the robot was stopped for 10 s and the chair was gently rotated clockwise or counterclockwise. When the participant tried to match the distance of the passive displacement, he/she moved leftward or rightward respectively. The 10-s delay was necessary to reduce to zero the endolymphatic circulation in the semicircular canals activated by the previous passive displacement and rotation (Young, 1984).

The experiment included 7 blocks of 6 trials each, for a total of 42 trials; 22 catch trials of 2 m and 4 m were intermixed; the 64 trials were performed in a

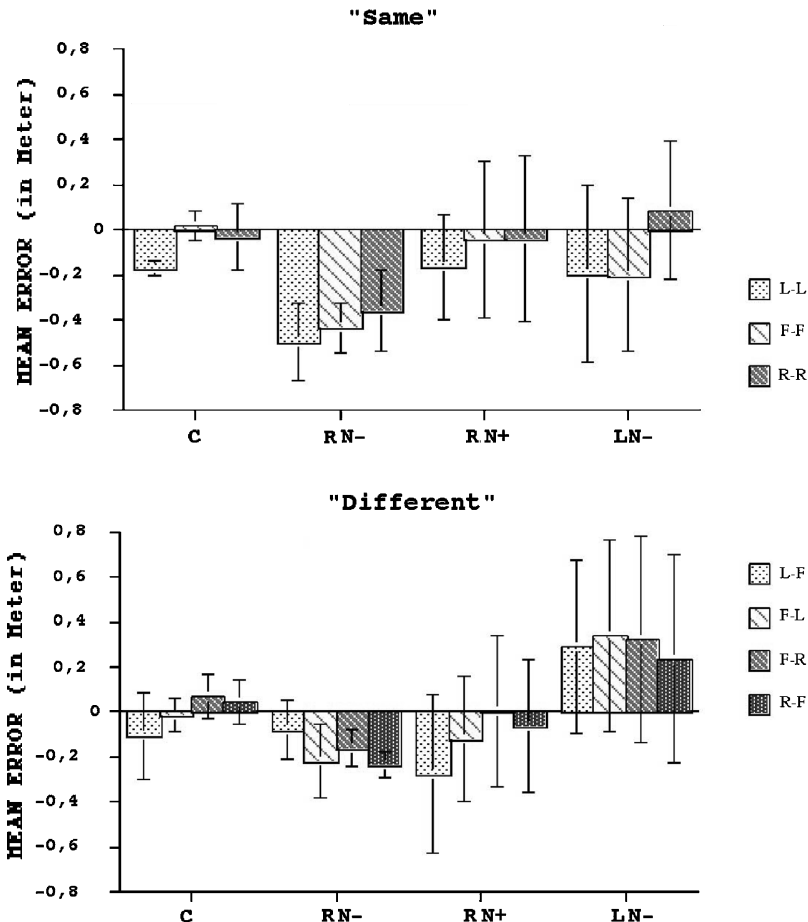


Fig. 2. Mean errors (and SD) for the same and different directions in the four groups. Positive and negative values indicate over- or undershooting the target, respectively.

Table 2. The Time (s) the Subjects Spent Actively Reproducing the Passive Displacement in Each Condition.

Group	Value	L-L	F-F	R-R	L-F	F-L	F-R	R-F
C	Mean	6.4	6.9	6.6	6.9	7	7.1	6.9
	<i>SD</i> error	1	1.6	1.4	1.5	8.1	1.7	1.2
RN+	Mean	8.5	9.4	9	8.3	9.3	8.8	8.4
	<i>SD</i> error	2.4	1.7	2.5	1.9	2.9	2.4	2.3
RN-	Mean	7.1	6.8	7.6	7.4	7.6	7.3	7.2
	<i>SD</i> error	2.2	1.4	1.4	2	2.3	1.1	9.3
LN-	Mean	10.6	9.5	9.6	10.6	10.6	10.5	10.9
	<i>SD</i> error	1.8	2.2	2.1	2.1	2.6	2	2.7

pseudo-random sequence. The measures of the participants' performances were errors (in meters) and time (in seconds).

### Time Estimation

The subjects were instructed to press a response button when the duration of the probe stimulus matched the duration of the reference stimulus. The probe stimulus disappeared when the button was pressed. The three reference stimulus durations were presented in a random sequence, 10 times each, for a total of 30 comparisons. The response time given by the participants was the dependent measure.

## RESULTS

### Linear Displacement

We analyzed the distances actively performed by the four groups for the different displacement directions. Figure 2 shows responses in terms of errors in reproduced distances. In the "same" and "different" condition, respectively, an analysis of variance group  $\times$  direction (distance as repeated measure) did not show any significant main effect (group:  $F(3, 16) = 0.607, p = .62$ ) (direction:  $F(6, 16) = 2.06, p = .06$ ) or interaction effect ( $F(18, 96) = 1.08, p = .37$ ).

The mean time of active displacement was submitted to an analysis of variance group  $\times$  direction (repeated measures), which showed a significant group effect ( $F(3, 16) = 4.41, p = .02$ ). A post hoc comparison (Duncan's test) revealed that the mean time used by the LN- group (10.32 s) was different from the C (6.83 s,  $p = .01$ ) and RN- (7.28 s,  $p = .01$ ) groups, but not from the RN+ (8.83 s,  $p = .18$ ) group. No other

between-group difference was observed. Table 2 reports the mean time and *SD* errors of all groups performing the active displacements in each condition.

The velocity profiles, indicating the capacity to process acceleration, were also analyzed. Figure 3 reports the average profile of the four groups. The control group matched the triangular shape of the velocity profile more closely than the brain-damaged groups, which were similar. The total distance covered, given by the surface under the curves, was the same, but the patients obtained these results with lower peak velocity and longer duration of motion. However, no difference was

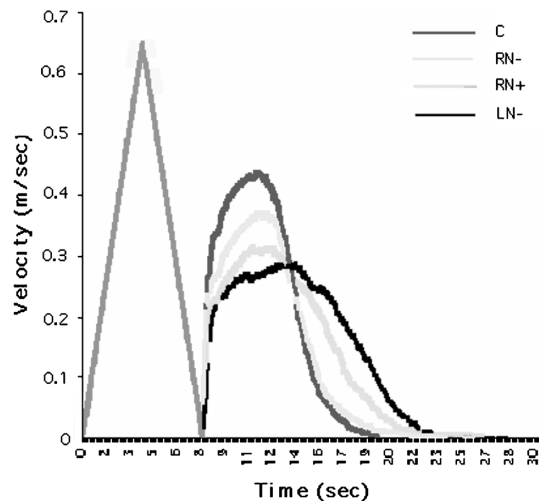


Fig. 3. The velocity profile of the passive translation on the left and the mean velocity profiles of active translations in the four groups on the right, pooling the different directions.

found in processing acceleration (and therefore in processing vestibular information) among the three groups of brain-damaged patients.

### Time Estimation

An analysis of variance group  $\times$  time replication (6, 8 and 10 s, repeated measures) showed a significant group effect ( $F(3, 12) = 9.59$ ,  $p = .003$ ). A post hoc comparison (Duncan's test) revealed that, compared to the other groups, only the RN+ group showed longer time estimation.

## DISCUSSION

The results clearly showed that on a distance replication task performed along the horizontal axis and predominantly relying on vestibular and somatosensory information, neglect patients responded similarly to both control and brain-damaged groups. Furthermore, they reproduced distance in a symmetrical fashion in both left and right sides of space. Neither of these two results can be explained by the neglect patients' worse time estimation.

It must also be noted that the horizontal symmetry was present not only in the "same" conditions, but also in the "different" ones. This was true when the participant had to encode a "passive" leftward or rightward displacement and then actively reproduce it forward, or when a lateral movement was "actively" produced to match a forward translation. These results agree with Bisiach, Pattini, Rusconi, Ricci, and Bernardini's study (1997) in which neglect patients were asked to point out their start position after linear translations and rotations. Using a laser pointer, the patients indicated their starting point after linear displacements of 3 m forward, followed by turns of 90° to the right and left side of the body. The authors did not find any asymmetries in task performance after left or right turns.

On the other hand, our results strongly contrast with previous findings in which line length duplication (Chokron et al., 1997) or endpoint duplication (Bisiach et al., 1994, 1996) performed in the visual modality consistently showed a marked leftward extension. Thus, the interpretation that

this visual anisotropy in hemineglect may represent "a directional disorder of the metric of the brain's representational medium" (Bisiach, 1999) cannot be extended to spatial computation in the nonvisual domain.

## EXPERIMENT 2

The previous results suggest that such a simple comparison of body spatial displacement is so easy that it can be achieved at a somewhat low level of vestibular processing. However, it can also be speculated that to uncover an anisometric performance, which characterizes the clinical features of neglect patients, nonvisual information has to be integrated with spatially relevant visual information.

For instance, we hypothesized that as long as perception and memory of translation are tested, involving only integration of vestibular inputs, the parietal cortex might not be involved. However, if the information regarding the performed distance requires the integration of vestibular, somatosensory, and gravitational information as well as time and velocity estimation with a visual landmark present in the space, some deficit can be expected. The hypothesis is that in neglect patients with spatial anisotropy, the condition in which integration between nonvisual and memorized visual spatial location is required will induce horizontal spatial asymmetry.

In the second experiment, we asked the subjects to perform a spatial replication task in which visual information had to be remembered and integrated in the absence of visual information.

## MATERIALS AND METHODS

### Subjects

This experiment was performed with the same four groups of participants as in Experiment 1.

### Stimuli

The same robot was used as in Experiment 1; it moved with the same parameters and response measurements as in the previous experiment. The participants were passively transported by the robot with eyes open in either horizontal direction from a visible target to a stop

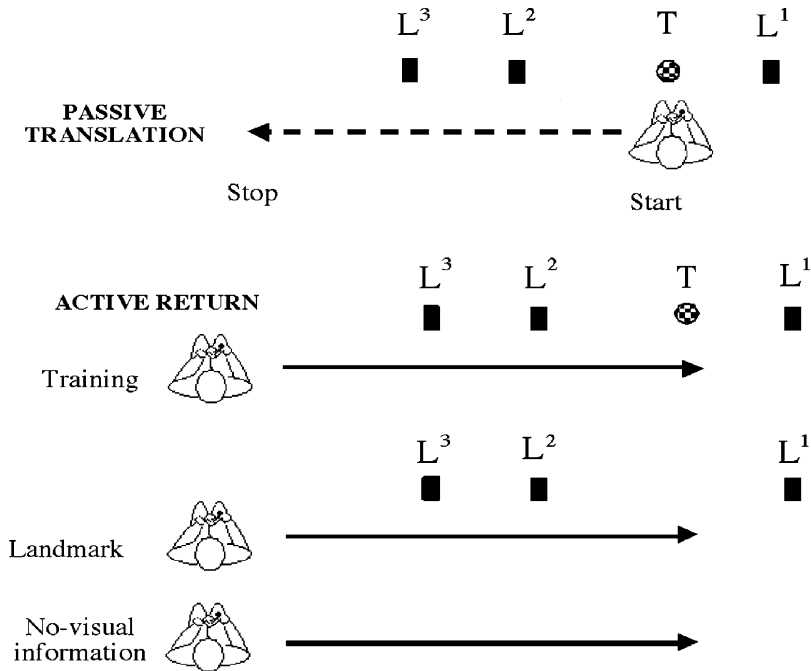


Fig. 4. Passive and active conditions:  $L^1$ ,  $L^2$ ,  $L^3$  = visual landmarks; T = target. The figure shows the case of leftward passive displacement and active returns toward the right side of the space. In the opposite condition, landmarks and target were arranged to produce a mirror configuration.

(Fig. 4). During the translation, they were able to see several visual landmarks and code the target position in relation to the landmarks. The task was to return to the target position in several different conditions (listed below). In all conditions, the subject's eyes were open in light, but target and landmark availability varied.

- (a) *Training*: during the "active return," all landmarks and the target were visible. Thus, this training did not require any computation or memory for location.
- (b) *Landmark condition*: the landmarks were visible, but the target was removed. The participants could memorize the position of the target in relation to the visible landmarks. The use of vestibular and somatosensory information may have been marginal.
- (c) *No visual information*: both landmarks and target were removed. The participants could combine the vestibular and somatosensory computation of the spatial transportation with recollection of the previously inspected target position by using visual mental imagery and updating the target position in a continuous, dynamic fashion (see Fig. 4).

We tested the hypothesis by comparing the landmark and the no visual conditions in the four groups of participants.

### Procedure

The participants were seated on the robot facing a long wall (9-m long) (Fig. 4) covered by a curtain. In this experiment, a red circle (target, T) 10 cm in diameter was attached to the curtain 150 cm from the end of the wall in the direction opposite to that of the passive translation. Three 12 cm  $\times$  21 cm cloth strips of different colors were used as landmarks. The first one ( $L^1$ ) was placed 40 cm from the end of the wall in the direction opposite to that of the passive translation. The other two landmarks ( $L^2$  and  $L^3$ ) were located 250 and 360 cm from the same end of the wall. Stimuli were arranged so as to produce a mirror configuration for two different directions of passive translations.

Starting in front of the target, the participants were passively displaced 3 m toward the left space, with the same velocity profile used in the previous experiment ("passive motion" in Fig. 4). The robot stopped for 10 s and the participants were prevented from seeing the manipulations of the target and the landmarks; then an acoustic signal indicated they had to press the button and return to the starting position ("active return

motion” in Fig. 4). The passive and active displacements were performed toward the left and the right space.

Twelve trials comprised the training, 6 for each condition and direction; 24 trials comprised the tests, 6 for each condition and direction. Both training and tests were administered in one session. The error in reproduced distance was considered the measure of the performance.

### RESULTS

The reproduced distance errors of the four groups are shown in Figure 5. An analysis of variance group (4) × condition (2) × direction (2) was performed, with the latter two variables as repeated measures. The principal effects of group and direction reached significance:  $F(3, 18) = 3.92$ ,

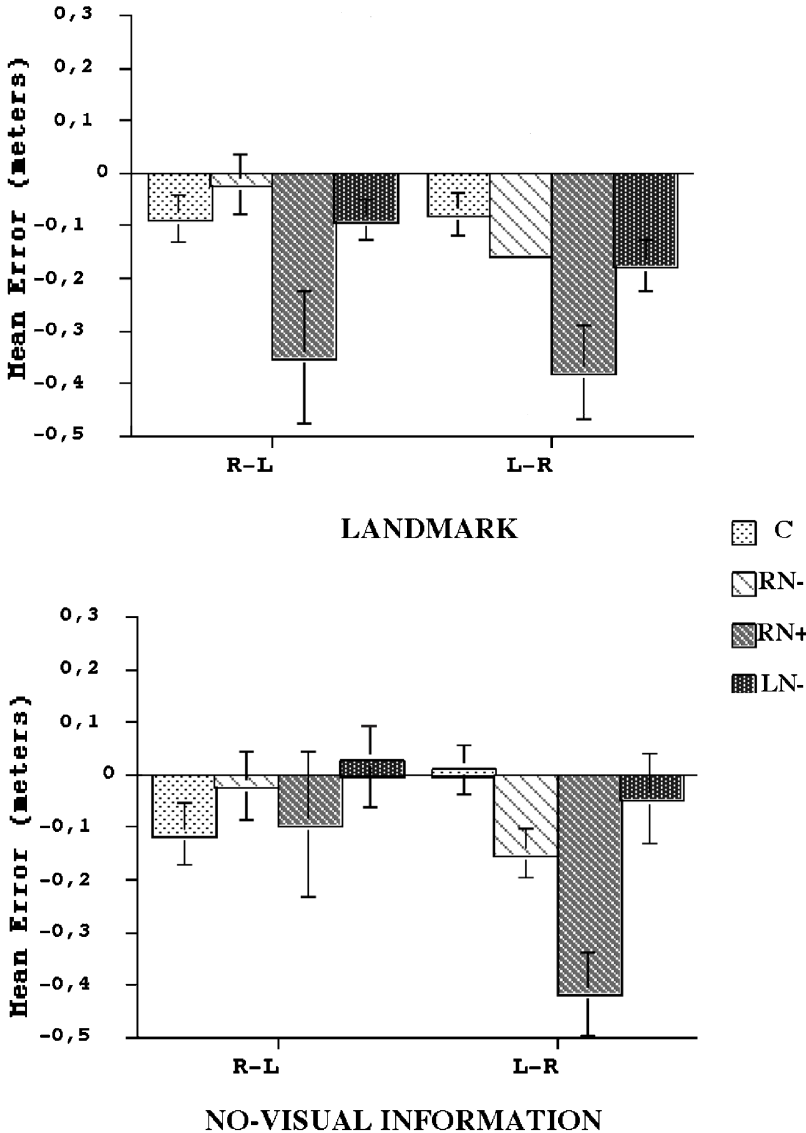


Fig. 5. Mean errors (and SD) for the four groups in the two conditions. R-L = passive displacement to the right, active return to the left side; L-R = passive displacement to the left, active return to the right side. Positive and negative values indicate the over- or undershooting of the target, respectively.

$p = .026$  and  $F(1, 18) = 3.51$ ,  $p = .048$ , respectively. A post hoc comparison (Duncan's test) showed that the RN+ performed active translations with more errors than the other three groups, which made a similar number of errors. All groups made more errors in active translations directed toward the right side.

The interaction group  $\times$  condition  $\times$  direction was also significant ( $F(3, 18) = 3.77$ ,  $p = .03$ ); a post hoc comparison (Duncan's test) showed that in the no visual information condition, right brain-damaged patients with neglect (RN+), at variance with the other groups, significantly reduced their undershooting when they actively moved toward the contralesional left space.

## DISCUSSION

Two different results emerged from the second experiment. When the task involved a minimal need to integrate vestibular and visuo-spatial information, there was no anisometry in any of the brain-damaged groups. Minimal integration means that the task can be performed on the basis of the remembered position of the target with respect to the landmarks, with reference to the two visual cues and with little attention to vestibular information.

Conversely, when the task relied heavily on vestibular and somatosensory information to provide an estimate of the amount of displacement, and also required memorizing the position of the previously seen target, the RN+ showed an unequal estimate of their movement toward the two sides of the space. Also, in the no visual information condition they continued to stop before the target, as in the landmark condition, when they actively moved rightward. On the other hand, they performed more accurately, that is, with marginal undershooting, when they actively moved leftward.

It can be hypothesized that neglect affects the ability to correctly code the metric relationships among environmental space, landmarks, and a target when they are perceived in the neglected hemisphere.

On the other hand, these results may be due to computing errors during the active leftward

movements. If this is the case, the error reduction probably depends on a trend to perform an overextension when moving toward the left side. In a sense, this is in agreement with duplication tasks previously used in the literature (Bisiach et al., 1994, 1996; Chokron et al., 1997) in which reproduction of a distance used a different metric in the left hemisphere, possibly due to an underestimation of this side of the space. Doricchi and Angelelli (1999) showed that this phenomenon is observed only when the neglect is associated with a contralesional hemianopia. In contrast, in the present test no neglect patients had hemianopia, although they still made greater leftward than rightward extension of their body movement.

In any case, the present data are not sufficient to verify whether neglect affects the coding of leftward space during passive leftward movements or whether it affects the computing of leftward active movements. Thus, further research is required comparing movements in the same directions.

The present results differ from those of a recent study (Philbeck, Behrmann, Black, & Erbert, 2000) showing the absence of left-right differences in a task of visually directed walking. This difference may be due to two different factors: (1) a more complex task was used in our experiment, requiring greater cognitive integration; (2) only some of Philbeck et al.'s patients (Philbeck et al., 2000) had neglect and all of them could walk (at variance with our sample in which no patient could walk) indicating they were affected by a different and perhaps less severe lesion.

## GENERAL DISCUSSION

If anisometry, with which the brain processes spatial information, is a basic feature of hemispatial neglect, we should expect it to cut across spatial representation independent of sensory inputs. In line with this prediction, previous findings showed the existence of a contralateral disorder in the nonvisual search for objects (Bisiach, Capitani, & Porta, 1985; De Renzi & Scotti, 1969) and in the location of auditory signals (Altman, Balomov, & Deglin, 1979; Bisiach, Cornacelia, Sterzi, & Vallar, 1984). The

present study explored the capacity to process spatial information by displacing the entire body in space, predominantly involving vestibular and somatosensory inputs. In these conditions, brain-damaged patients performed as well as normal controls (Exp. 1) on a task involving the reproduction of a passive translation on a horizontal or a sagittal plane. Furthermore, no asymmetrical performance emerged even when the active reproduction was carried out in a different direction than the previous passive transportation. This result can be interpreted in two ways. First, since the CNS does not have a system to directly measure a displacement of the entire body, the estimate can be made only by computing the distance, combining velocity and time. The error involved in this measure might be so great that any potential difference disappears. It is certainly true that this estimate is not as accurate as visual measurements, but the percentage of error over the total body displacement ranges from 10 to 20%, similar to other nonvisual (proprioceptive or acoustic) measures. Also, the good consistency of responses across trials in the same subject suggests that these measures are sufficiently reliable.

The other possibility is that the different levels at which the successive vestibular and somatosensory information can be compared (i.e., the vestibular nuclei in the brain stem, the thalamus, and different cortical areas; Grüsser et al., 1992) do not show any of the functional asymmetry shown for complex visual processing. The few existing neuroimaging studies in humans, which did not involve the cortical representation of vestibular information, showed such asymmetry (Lobel et al., 1998).

However, the data of the second experiment showed anisometry in neglect patients with right brain damage when replicating distances on the horizontal plane. On one side, a cognitive analysis of the nonvisual information condition of this experiment required computation of the distance to be reproduced on the basis of vestibular and somatosensory inputs and, on the other, memory of the location of the previously inspected landmarks and the target. Thus, the two categories of information must be integrated in some cortical areas.

According to Grüsser et al. (1992), there are no direct connections between the primary visual cortex (V1) and the vestibular cortical areas (PIVC). Therefore, the integration between visual and vestibular inputs must take place on one of the two following pathways: (a) from V1 to V2, MT-MST, parietal area 7 and then to the parietoinsular vestibular cortex (PIVC) or (b) from the superior colliculus, pulvinar, thalamus to the PIVC. It can be speculated that some asymmetry in evaluating spatial displacement occurs only when one or both of these networks connecting visual and vestibular information are damaged.

The task also required the subjects to memorize a spatial location of the target in particular relation to three visual cues (see the two test conditions of Exp. 2). In order to respond to this task, the subject had to refer to the relative position of both the target and the landmarks in space. Thus, the subject was strongly encouraged to use an object-centered frame of reference.

In a recent fMRI study, Galati et al. (2000) showed that when normal subjects respond to a spatial task by using an object-centered frame, strong asymmetrical activation of a right parieto-frontal system occurs.

It can be suggested that the spatial anisometry in processing movements of the whole body in space, which emerges following a brain lesion, can be observed in two conditions:

- (1) when the spatial computation requires a multisensory integration of the vestibular, somatosensory and mental representation of the visual information;
- (2) in the presence of brain lesions most frequently producing such anisometry, which are located in the right hemisphere and produce the neglect syndrome.

More specifically, the lesion could be located in the parietal lobe, disconnecting the pathway that indirectly connects the striate cortex with the PIVC area, or in areas involved in the connection of the superior colliculus to the PIVC, via the pulvinar and the thalamus. In line with these observations, a perusal of the participants' lesion sites (see Table 1) shows the involvement of the right supramarginal and angular gyri (Brodmann's

areas 39 and 40) in those participants whose performances showed signs of anisometry (i.e., RN+ who reduced errors in the contralesional active translations). These areas are preserved in the RN-, but are lesioned in some LN-, demonstrating the specific involvement of the right hemisphere in anisometric defects.

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