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Perception of biological motion in parietal patients

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Abstract

Three unilateral parietal patients were tested on their perception of biological motion, a special case of form-from-motion. Two patients had the lesion in the right, and one in the left parietal area. All patients could easily perform a classical form-from-motion task [Neuron 32 (2001) 985], but they were severely impaired in a visual search task using biological motion sequences. In particular, the left parietal patient showed a more severe loss. He was unable to identify even a single item. Overall our patients seemed to perform differently from the classical motion-blind patients described in the literature [Visual Cognition 3 (1996) 363; Eur. J. Neurol. 9 (2002) 463; Visual Neurosci. 5 (1990) 353] whose lesions included the visual cortical area V5. Since our patients' low-level motion mechanisms are preserved, we suggest that the perception of biological motion relies on a high-level description of dynamic patterns [Cognition 80 (2001) 47], a mechanism that is impaired in parietal lobe patients. We discuss our results at the light of the recent theories suggesting that biological motion is performed by visual associative areas outside the classical motion pathways and that it is an active process dependent on attentional resources [Cognition 80 (2001) 47].

Keywords: Parietal lesion; Left neglect; High-level motion

1. Introduction

Right parietal patients often exhibit left visual neglect, a striking deficit of orienting visual attention to stimuli presented on the side contralateral to the lesion (Vallar, Rusconi, Bignamini, Geminiani, & Perani, 1994; Vallar, 1993). Neglect is usually present in the acute stage after a stroke. In the chronic stage, patients are more likely to exhibit visual extinction, a deficit that manifests mostly under experimental conditions (or at clinical confrontation) (Vuilleumier & Rafal, 2000). In this case the patient fails to detect a stimulus in the contralateral field when it is simultaneously presented with a similar stimulus in the opposite visual field. Performance is normal in both visual fields when one stimulus at a time is presented. One paradigm that is typically used to study attentional mechanisms both with normal subjects and with parietal patients is visual search (Arguin, Joanette, & Cavanagh, 1993; Esterman, McGlinchey-Berroth, & Milber, 2000) where observers are asked to detect or discriminate a target item among distractors. Right parietal patients' performance is generally normal when they are asked to perform a simple search task (say, finding a red target among green distractors), while they are impaired in more difficult searches when attentional resources must be allocated to each display item in turn (Laeng, Brennen, & Espeseth, 2002).

While a great deal of research has tested the visuo-spatial abilities of neglect patients, both in vision (Duncan et al., 1999; Vuilleumier & Rafal, 2000) and audition (Bellmann, Meuli, & Clarke, 2001; Griffith et al., 1997), much less is known about their perception of motion. Conversely, visual motion perception in parietal patients has rarely been studied (Braun, Petersen, Schonle, & Fahle, 1998; Greenlee, Lang, Mergner, & Seeger, 1995; Greenlee & Smith, 1997; Schenk & Zihl, 1997) and the exception is a large body of work that has concentrated on 'motion-blind' patients who are usually affected by bilateral lesions involving the human homologue of motion area V5 (McLeod, Dittrich, Driver, Perrett, & Zihl, 1996; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990; Zihl, von Cramon, & Mai, 1983) with no involvement of the parietal cortices. One particular kind of motion pattern is biological motion, which has also been defined as a special case of shape from motion (Grossman & Blake, 1999). Patients affected by V5 lesions have been extensively studied on biological motion perception (McLeod et al., 1996; Vaina et al., 1990), in some cases using the same point-like walkers originally used by Johansson (1973) in his first demonstration. The original Johansson figures were created by attaching lights (or reflective tape) to the major joints of the body of human actors, who were then filmed

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under dim light conditions so that only the lights were visible. The actors then performed different actions: standing up from a chair and walking, climbing up the stairs, painting a wall, people hugging, performing push-ups or dancing. Even though only a few point-lights are visible, the overall configuration gives a compelling impression of human actions. Johansson pointed out that the perception of a walking person in the motion of 10 dots seems to be equally spontaneous and natural as seeing a real man walking (Johansson, 1973). The author suggests that such fluent perception might be the consequence of prior learning in seeing human walking. Indeed it is surprising how even naïve subjects can so easily perceive human walking from a set of moving dots and the motion pattern always evokes a spontaneous and compelling response of a walking human being.

Several studies have examined whether attention is necessary to process biological motion (Cavanagh, Labianca, & Thornton, 2001; Heptulla Chatterjee, Freyd, & Shiffrar, 1996; Thornton, Rensink, & Shiffrar, 2002) or whether low-level visual processing alone (Mather, Radford, & West, 1992; Thornton, Pinto, & Shiffrar, 1998) is sufficient. It has been recently demonstrated (Cavanagh et al., 2001; Thornton et al., 2002) that although the detection of biological motion mimicking human walking seems effortless, it actually demands attention. This has been demonstrated using a visual search task in which subjects detected the presence of a walker facing opposite to the distractor walkers or a walker among jumbled walkers. In the present report we used the same task with our parietal patients (Cavanagh et al., 2001) in an attempt to see whether changing the attentional load with the number of distractors would affect their performance.

Recent work has shown that lesions to area V5 affect the perception of biological motion when the stimulus is presented in noise. McLeod et al. (1996) tested LM, a patient with a bilateral lesion of the V5 areas. LM was unable to distinguish normal from jumbled biological motion in the presence of static visual noise (dots), whereas she could easily perform the task without the visual noise. In contrast, the parietal patients we tested had difficulty in distinguishing a walker among jumbled walkers when presented simultaneously, even in absence of background noise. We manipulated the tasks so that the subjects could not make the discrimination based only on a single static frame, as in the original Johansson (1973) figures where occlusion cues could suggest posture and direction of motion on a single static frame. Instead, in our task it was necessary to integrate the velocity and direction of several moving dots in order to discriminate the human walker. The patients were first tested using the original walkers of Johansson (1973) and we simply asked them to tell us what they saw on the monitor without any further instruction. We subsequently tested them on two visual search tasks using biological motion.

Bilateral parietal patients have previously been tested on biological motion perception (Schenk & Zihl, 1997). The two patients who were tested showed a loss in the ability to determine whether a single test figure was a walking person or a scrambled figure when the test was embedded in noise but showed no deficit without the noise. In another study (Regan, Giaschi, Sharpe, & Hong, 1992), unilateral parietal patients were impaired in a form-from-motion task when asked to identify a motion-defined letter. The authors in these two studies claim that the superior parietal cortex is involved in form-from-motion perception and that it might serve complex perceptual tasks requiring the integration of different motion signals as in the case of biological motion.

Indeed, Schenk and Zihl (1997) also argues that a deficit to an attentional mechanism contributes to the impaired performance on biological motion perception in the parietal patients. In the present study although there is some variability among the patients' results, we demonstrate that unilateral parietal patients have difficulties in identifying single "walkers" in biological motion (the left parietal patient) and in performing visual search tasks with multiple walkers (right parietal patients).

The same patients are impaired in the field contralateral to the lesion on tasks of visual tracking (Battelli et al., 2001) and in the perception of apparent motion in both visual fields (Battelli et al., 2001). A recent study by Thornton et al. (2002) has shown that attention related mechanisms are used during biological motion perception and that they depend on the temporal feature of the stimuli. Because of the previous evidence of deficits for tasks requiring temporal attention in parietal patients such as the ability to perceive apparent motion (Battelli et al., 2001) or disorders in discriminating events presented at high temporal frequency (Husain, Shapiro, Martin, & Kennard, 1997) we felt that the losses, if any, in the perception of biological motion in parietal patients could help us understand the role of temporal attention in this task.

2. Methods

2.1. Case histories

We tested three stroke patients: JR, JL and JS. JR and JL had unilateral, right parietal lobe lesions with some extension into surrounding structures, while JS had a left parietal lesion. Magnetic resonance images (MRIs) were analyzed to define the anatomical distribution of the lesions using the Damasio atlas (Damasio, 1995). Two subjects, one male and one female with no history of neurological disease served as age-matched normal controls.

Patient JL, a 62-year-old right-handed man, suffered a left occipital lobe hemorrhage in 1998 and a right parietal hemorrhage in 1999. The first stroke presented with symptoms of right hemianopia, which gradually recovered, and the second with left hemianopia, which has not improved. Nine months after his second stroke, MRI revealed right-sided signal abnormalities involving the superior parietal lobule, angular

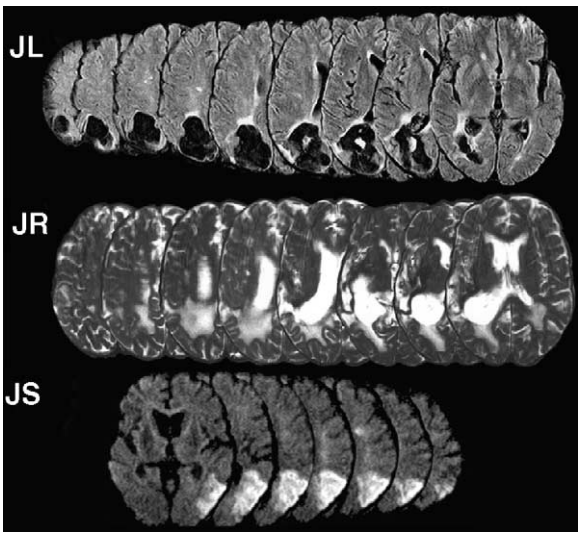

Fig. 1. Horizontal MRI sections through the cerebral hemispheres of the three stroke patients with unilateral lesions are shown here. Flair images for JL and T2-weighted images for JR are reported. JL and JR had extensive lesions of the right lateral occipital, supramarginal, and angular gyri, as well as the precuneus and the superior parietal lobule. Pre-existing white matter lesions are also evident in JR. JS's diffusion weighted images are reported. He had an infarct of the left angular and supramarginal gyri.

gyrus, supramarginal gyrus, precuneus, cuneus, and lateral occipital gyri (Fig. 1). There was no imaging evidence of his prior left-sided lesion. We first tested JL 11 months after his second stroke. He complained that his vision looked "watery" and that stationary visual objects were jumping and moving. Examination revealed a left inferior quadrantanopia. Visual acuity with correction was 20/40 in his right eye and 20/25 in his left eye. On the Sunnybrook neglect battery (Black, Vu, Martin, & Szalai, 1990) JL scored 40/100, indicating severe left hemispatial neglect.

Patient JR, a 70-year-old right-handed man, was admitted to the hospital in October 1998 with left hemispatial neglect, left superior quadrantanopia, normal visual acuity, and left hemiparesis. CT revealed a hemorrhage involving deep and superficial right parietal lobe and temporal lobe structures. Ten months later, MRI showed extensive signal abnormalities involving the right superior parietal lobule, angular gyrus, supramarginal gyrus, precuneus, lateral occipital gyri, and middle temporal and superior temporal gyri (Fig. 1). We first tested JR 8 months after his stroke. On the Sunnybrook neglect battery (Black et al., 1990), JR scored 10/100, indicating mild residual left hemispatial neglect.

Patient JS, a 67-year-old right-handed male, suffered a stroke in July 2000. MRI diffusion weighted images revealed an infarct of the left angular and supramarginal gyri (Fig. 1). At the time of testing he had a right hemianopia. On the Sunnybrook neglect battery (Black et al., 1990) he scored 30/100, indicating mild right hemispatial neglect. During the testing sessions all the stimuli were presented bilaterally in the left and right parafoveal fields, both of which were intact in all patients.

2.2. Apparatus

The experiments were conducted on a G4 laptop computer connected to an Apple Studio Display. Software for all the experiments were written in Think C™. For experiment 1 we used programming routines (Shell™) created by Raynald Comtois (http://www.visionshell.com). The same basic equipment was used in all experiments.

2.3. Experiment 1: low-level motion

The task employed in this experiment is often used with patients to test low-level motion perception abilities (Vaina et al., 1990). The target is a motion-defined rectangle presented on a background of randomly moving dots. In a two alternative forced-choice procedure the subject has to report the orientation of the rectangle that can be either horizontal or vertical. Although attention is necessary to report the orientation of the shape defined by multiple dots coherently moving in the same direction (Newsome & Paré, 1988), the motion analysis that defines the shape is carried out effortlessly and automatically (Cavanagh, Arguin, & Treisman, 1990). Many neuropsychological cases have previously been reported of patients with deficits in low-level motion task similar to the one we used here. The cerebral lesions of these patients are more often located in the extrastriate motion areas, such as V5 or V3 (Greenlee & Smith, 1997; Plant & Nakayama, 1993; Vaina, Makris, Kennedy, & Cowey, 1998; Zihl et al., 1983).

2.3.1. Stimuli and procedure

In this task we measured the ability of the subject to perceive two-dimensional shapes generated by a difference in motion coherence of the target dots compared to the background (Fig. 2A). The background consisted of randomly moving black and white pixel dots of 50% density and a mean luminance of 60 cd/m^2. The dots moved at a velocity of 3°/s. On each trial the subject had to identify the orientation of a rectangle (subtending $7.5 \times 4.3^\circ$) presented for 450 ms in one of the hemifields, randomly across trials. Within a two alternative forced-choice procedure the subject had to report whether the target rectangle was oriented horizontally or vertically. The difference (the percentage of dots coherently moving in the same direction) between the shape and the background was varied randomly across trials. The percentages of coherence differences tested were: 20, 35, 50, 65, 80 and 95. The stimuli were presented in blocks of 72 trials for each hemifield (12 trials each level of coherence, a total of 144 trials) randomly ordered, with 15 practice trials preceding the beginning of the experiment.

2.4. Experiment 2: gait discrimination

We next tested the patients on the perception of point-light walkers engaged in simple activities and then on visual

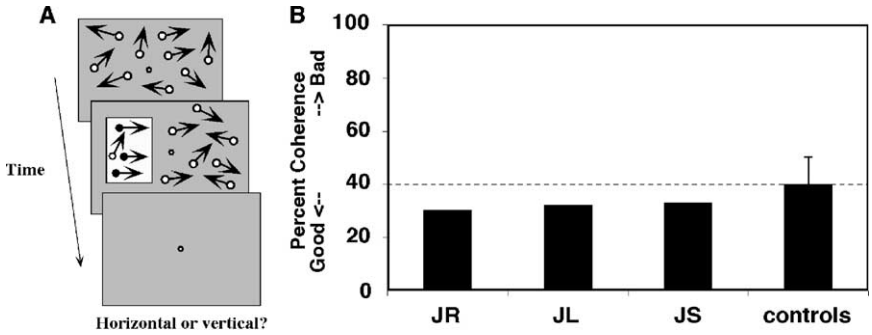

Fig. 2. (A) An example of the sequence of the task is given. Here the target is a rectangle (here depicted with outline contours not present in the actual task) presented for 450 ms in the left field (middle panel). The filled dots indicate the signal dots all coherently moving in the same direction. The arrows indicate motion and they were not present in the actual stimulus. (B) Percent of dot coherence at which the subjects perform 75% correct are reported for each patient: JR, JL (data from Battelli et al., 2001) and JS, and a group of three age-matched controls. Lower coherence threshold indicates better performance. Average threshold was 40 (±10.5) for age-matched control and 31.76 (±1.3) for the patients. The dotted line indicates the average performance of control subjects. On the *y*-axis the arrows indicate good and bad performance.

search through arrays of multiple walkers or scrambled walkers. In the first phase we used the original Johansson (1973) movie clips in which different point-light human walkers walk, climb, hug, ride a bicycle, do push-ups and, we asked the patients what they saw without any further instruction. The two right parietal patients JL and JR could recognize all the figures and the actions, although it took a relatively long time to do so. In particular JL, when first presented with the stimuli, reported only that there were a few dots moving on the monitor in an oscillating (pendulum-like) pattern. Only after several presentations did he recognize the biological motion, although it remained difficult for him to report the different actions. The left parietal patient JS showed a more severe loss. He was able to identify the human walker in the stimuli only after suggestions from the experimenter. Even when he did identify the walker, he was very slow (about 1 min) and he was not able to determine how many walkers (when more than one) or recognize the different actions (i.e. he reported the person riding a bicycles as someone running).

In the next phase, we used a visual search procedure (Cavanagh et al., 2001) to examine the role of attention in perceiving the biological motion for these patients. In such tasks, from one to four figures can be presented simultaneously and the subject must report if there is a walker among scrambled figures or one walker headed, say, to the left among distractors walking to the right. Results from normals (Cavanagh et al., 2001) show that each figure has to be analyzed in turn to identify a walker or its direction. Thus even though the perception of the figures seems effortless and rapid it is actually a serial process requiring attention focused on a single walker at a time. Given the deficits of parietal patients in attention, we expected some losses in this task for the three parietal patients. Indeed, patient JS with a left parietal lesion was unable to respond well enough to participate in this task, even following practice. Therefore in Section 3, only the data from JL and JR are reported together with those of the age-matched controls.

2.4.1. Stimuli and procedure

The biological motion configuration was generated by modifying Cutting's classic point-light walker algorithm (Cutting, 1978). The set of 11 dots simulated a walker seen in profile with lights on the head, near shoulder, both elbows, both wrists, near hip, both knees and both ankles. The dots were always visible to avoid providing non-motion cues to direction by occlusion clues (Thornton et al., 2002) (Fig. 3A). The walker walked in place as if on a treadmill with either left- or rightward gait. The distance from the fixation to the center dot of the walker subtended about 4° of visual angle, as did the height of the walker. The maximum stride width of a walker was about 2° of visual angle. The dots themselves had a diameter of 0.2° of visual angle. The walker's stride cycle took about 1.3 s, falling within the range of 0.8–2 s per stride reported for normal human walking (Inman, Ralston, & Todd, 1981). The walker's starting phase in its stride and position around the fixation point was randomly assigned on each trial. When more than one walker was displayed, the starting phase of the stride for each was assigned randomly and spaced equally around fixation. The dots had a luminance of 11.4 cd/m^2, and were presented on a 28.3 cd/m^2 background. The fixation mark was a black cross at the center of the display subtending 0.5° of visual angle. The subject sat at 60 cm from the monitor and they were instructed to hit one of two keys to indicate whether the target was present or absent as soon as they knew the response. If they did not respond within 8 s the trial was terminated. The number of correct responses and reaction times were measured. A total of 80 trials were run, with 10 trials for each condition (present or absent) and for each distractor numerosity (1, 2, 3 and 4). Ten practice trials were run preceding the beginning of the experiment. Two versions of the biological motion task were tested. In this experiment the subjects were asked to determine whether a rightward gait person was present among leftward gait persons, while in experiment 2b the subjects were asked to detect a walker among non-walkers.

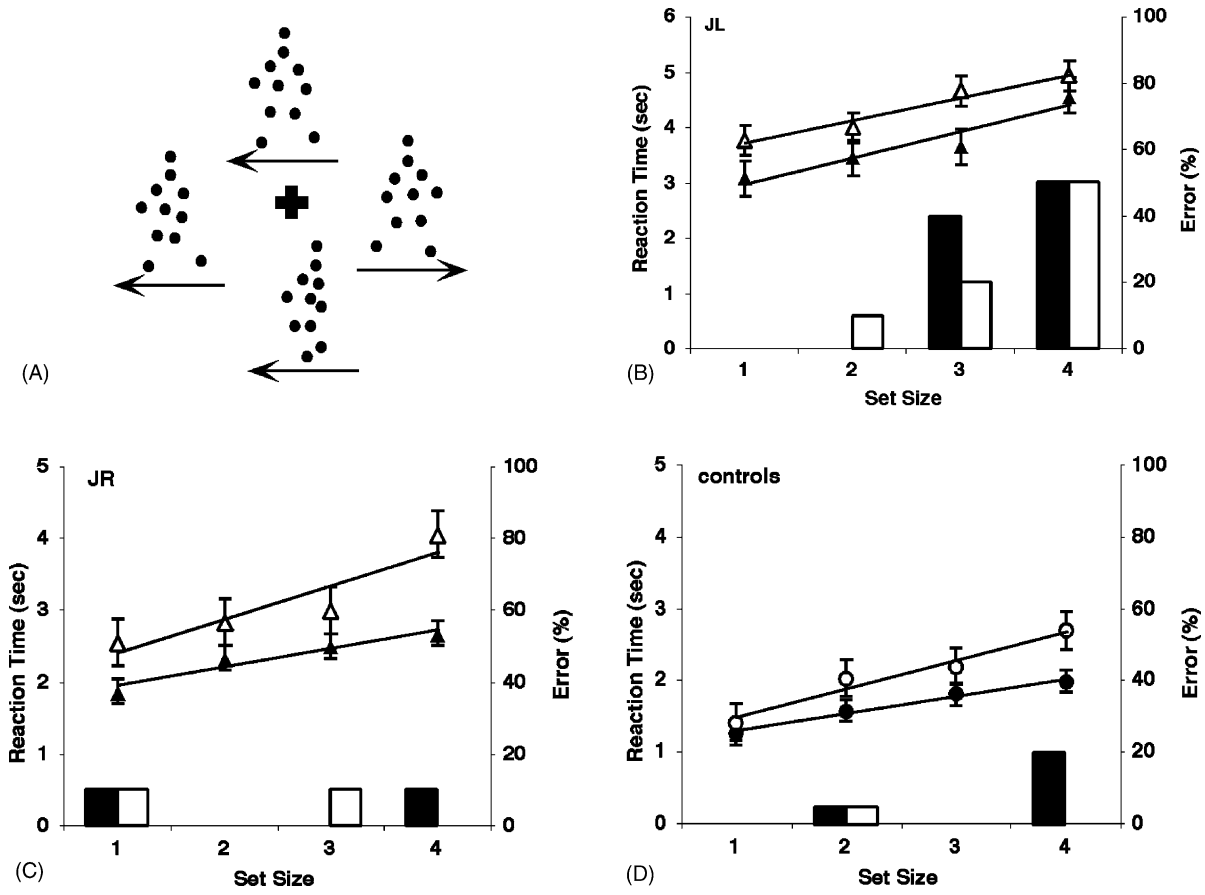

Fig. 3. (A) A static frame from a display with four walkers. The target walker is a figure walking to the right. The arrows indicate motion but they were not present in the actual stimulus. (B–D) Reaction times in seconds (left vertical axis) are reported for correct responses for present (filled symbols) and absent (outline symbols) trials for JL, JR and two age-matched control subjects. The solid lines show the linear regression for each data set. Percent of errors is reported on the right-hand axis and is shown as filled bars for target present and outline bars for target absent. Vertical bars represent the standard error of the mean (±1S.E.).

2.5. Experiment 2b: normal versus scrambled walkers

2.5.1. Stimuli and procedure

The stimuli, method and procedure were the same as those used in experiment 2 except that the subject's task was to find the presence of a normal walker among scrambled impossible walkers. These were obtained by shifting out of phase the dots of one arm and of one leg relative to the rest of the body. The overall configuration (in terms of distance between the dots and therefore size of the stimulus) remains the same as in the normal walker but the motion pattern is altered and the normal walking is compromised (Ahlström, Blake, & Ahlström, 1997).

As in experiment 2, when more than one walker (or non-walker) was displayed, the starting phase of the stride for each was assigned randomly and spaced equally around fixation. Within a two alternative forced-choice procedure the observer had to report whether a normal walker was present or absent. Reaction time and percentage of correct responses were measured. Ten practice trials were also run preceding the beginning of the experiment. A total of 80 trials were run, with 10 trials for each condition (present or absent) and for each distractor numerosity (1, 2, 3 and 4).

3. Results

3.1. Experiment 1: low-level motion

All three unilateral patients performed the task-like age-matched normal controls (Fig. 2B). Results for JR and JL have previously been reported elsewhere (Battelli et al., 2001) and here they have been contrasted to the left parietal patient JS. The patients were tested both in the left and right visual field and since there was no significant difference between hemifields the data in the graph have been collapsed. From this experiment we can conclude that our patients can perform a low-level motion task effortlessly. Conversely, V5 patients fail in tasks similar to this (Vaina et al., 1998), for instance, they fail in low-level motion tasks where they are asked to detect motion of a small number of dots coherently moving within a dynamic background. They

perform normally in motion segmentation tasks when the background is stationary (Vaina et al., 1990) or when there is only a low-level of background noise (Rizzo, Nawrot, & Zihl, 1995). Finally, although in our form from motion task attention is required in order to notice and report the shape of the rectangle, the motion that defines the shape does not require attention for the shape to become visible. This has been demonstrated in a visual search task (Cavanagh et al., 1990) where the speed to detect a vertical, motion-defined rectangle in a field of horizontal, motion-defined rectangles (distractors) was unaffected by the number of distractors.

3.2. Experiment 2: gait discrimination

First recall that the left parietal patient JS was so impaired at the perception of biological motion that he was unable to participate in this experiment. Reaction times for correct trials and percent errors are reported for right parietal patients JR and JL in Fig. 3B and C, respectively. Average data from two age-matched controls are reported in Fig. 3D.

Confirming previous studies (Cavanagh et al., 2001), the results show that the search was serial both for the patients and the control subjects. The target walker did not pop-out and each figure required individual scrutiny to determine the presence or absence of the target. The overall error rate was 21.2, 5 and 3.75% for JL, JR and the controls, respectively. Slopes for target present and absent were calculated. The search rate for the two age-matched controls was 166 and 209 ms per item for target present and absent, respectively. The search rate for JL was 369 and 434 ms, while for JR it was 235 and 312 ms per item for target present and absent, respectively. In terms of mean reaction time across all trials, the patients took twice the time of the controls to find the target among distractors. JL was very slow but accurate on trials where only one or two stimuli were present, confirming that he could discriminate the human walker if given enough time. His performance fell close to chance on trials with more than two stimuli. JR performed better than JL, although he was significantly slower than controls.

3.3. Experiment 2b: normal versus scrambled walkers

Results are reported in Fig. 4. For the normal controls, reaction times again increased as a function of the number of distractors indicating a serial search processing. All the subjects reported this task was more difficult than experiment 2 and the results confirmed this observation.

The overall error rate was 53.7, 21.2 and 2.5% for JL, JR and the controls, respectively. Slopes for target present and absent were calculated. The search rate for the two age-matched controls was 186 and 229 ms per item for target present and absent, respectively. The search rate for JL was 388 and 452 ms, while for JR it was 297 and 371 ms per item for target present and absent, respectively. Both JL and JR had more difficulties in performing this task. In particular JL was completely unable to determine whether it was a normal walker or a jumbled one even during trials with one stimulus. We calculated A' to determine the criteria JL adopted to perform the task. A' is a measure of sensitivity very similar to d' but more accurate in characterizing performance with yes/no paradigm (Donaldson, 1993; Macmillan & Creelman, 1991). It increases from 0.5 for chance performance to 1.0 for perfect performance. We measured A' for JL at all set size and results indicated that he was never above chance ($A' = 0.5$ at all levels). Although his performance seemed better in the target present trials than in the absent, A' measure showed that JL was producing consistently more false alarms and, therefore answering present on most of the absent trials. JR performed better than JL but he was significantly slower than controls as can be seen in Fig. 4C.

We did not monitor eye movements during task presentation and since maximum exposure time was 8 s, subjects were free to fixate each figure in turn to determine whether the target was present or absent. With uncontrolled viewing, there is little or nothing to be gained from analyzing the data separately for trials with target left or right of the nominal fixation point. If there is a left versus right field difference in performance for our patients, they are free to fixate to one side or the other of each walker in order to place the items in the good field. There is evidence that this refixation strategy is used by right parietal patients (Husain et al., 2001). Any performance loss with free viewing therefore probably reflects a loss in both fields. We have previous data from the same patients (Battelli et al., 2001) showing that they were impaired in both visual fields in tasks of visual timing, whereas the same patients presented only a contralateral deficit in selective and sustained attention tasks.

It is well known that parietal patients show deficits for difficult visual search tasks, involving conjunctions (for example, Esterman et al., 2000). However, our data demonstrate that the poor performance we see here for biological motion is not another example of the loss for conjunction search. In particular, the pattern of data for the biological targets differed markedly from that for previously tested conjunction targets at set size one, when there is a single item in the display. Both JR and JL have very high reaction times and significant errors (in experiment 2b) at set size one showing that patients can have difficulty with even a single target (either on the left or on the right visual field). Data reported in the literature on difficult visual search tasks with parietal patients never show significant error rates at set sizes lower than four items (Esterman et al., 2000) on bilateral presentations. The effect of the parietal lesions is typically to increase the slope of the reaction time function and the rate of increase of errors with additional distractors but not to affect performance, relative to controls, with a single item in the display. Furthermore, left neglect patients have no difficulty if target and distractors are presented within a single field, either right or left (Robertson & Marshall, 1993). These results suggest that our visual search tasks with biological motion must be calling upon mechanisms

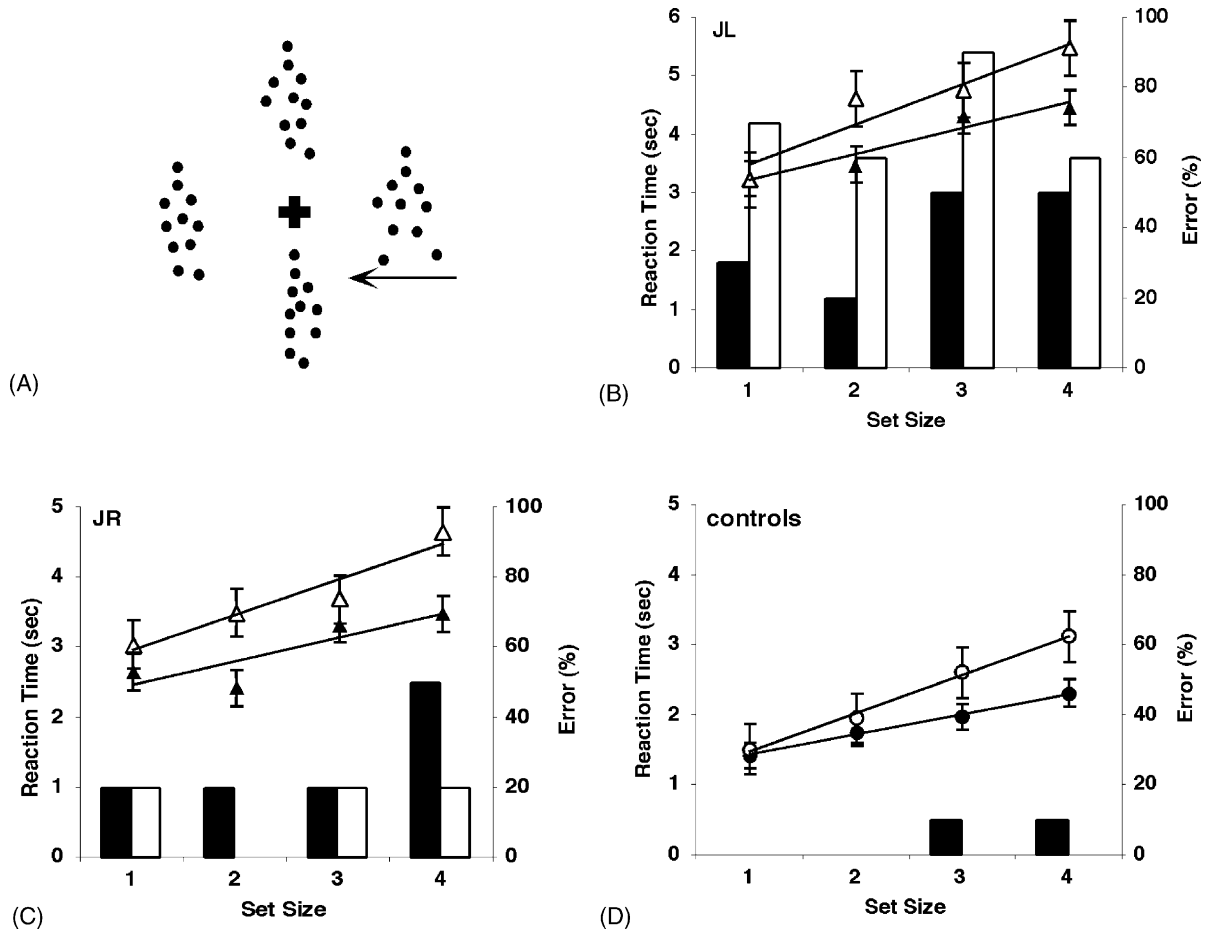

Fig. 4. (A) A static frame from a display with four stimuli: one normal (the target) and three jumbled walkers that resembled moving puppets. The arrow indicates motion but it was not present in the actual stimulus. (B–D) Reaction times in seconds (left vertical axis) are reported for correct responses for present (filled symbols) and absent (outline symbols) trials for JL, JR and two age-matched control subjects. The solid lines show the linear regression for each data set. Percent of errors is reported on the right-hand axis and is shown as filled bars for target present and outline bars for target absent. Vertical bars represent the standard error of the mean (±1S.E.).

beyond those required in a common conjunction visual search task.

4. General discussion

This study provides important findings about the deficits in unilateral parietal patients in the attentional abilities required to detect biological motion. Furthermore, it gives important insights about how the visual system analyzes biological motion. According to our previous study with bilateral and right parietal patients (Battelli et al., 2001) and, confirmed by the present results that include a left parietal lesion subject, low-level motion perception is intact in these patients. They can easily segregate a coherently moving pattern within a high level of background noise, profoundly different from the results for V5 patients reported in the literature (Rizzo et al., 1995; Vaina et al., 1990).

Biological motion displays present complex configurations in which groups of oscillating dots moving along different trajectories at different speeds must be combined together in the appropriate geometry to give the strong impression of human actions. That is, they require an integration process that can link the unconnected traces (like assigning the knee dot and the ellbow dot to the same person walking on a treadmill) to generate a unitary percept, a global percept of a human walker. This latter integration process could be the operation that is disrupted in our patients, in particular in experiment 2b, where subject attempted to distinguish a jumbled from a normal walker.

Finally, the ability of V5 patients to recognize the original Johansson figures has been considered as a demonstration of their intact ability to see biological motion (Vaina et al., 1998; Vaina, Cowey, LeMay, Bienfang, & Kikinis, 2002). However, V5 patients have never been tested for biological motion in a visual search paradigm and they may yet show a deficit here. Nevertheless, our patients clearly perform differently from V5 patients in biological motion perception. In particular the ‘motion-blind’ patient LM (McLeod et al., 1996), can identify jumbled from normal point-lights walker

without static background dots. Our patient, JL cannot do so, as shown by his perfomance in experiment 2b when only one element is present on the display. JR conversely can do the task at set size one although he is extremely slow and his performance is close to chance with three distractors.

Parietal patients usually do not report having difficulties with visual motion, however during pshycophysical testing they show severe impairments in high-level motion tasks (Battelli et al., 2001) such as attentive tracking (Shioiri, Cavanagh, Myamoto, & Yaguchi, 2000; Verstraten, Cavanagh, & Labianca, 2000) or apparent motion perception (James, 1890/1950) and, it has been suggested that these tasks call upon attentional mechanisms (Esterman et al., 2000; Verstraten et al., 2000). It is very well documented in the literature (Duncan et al., 1999; Posner, Walker, Friedrich, & Rafal, 1984; Robertson & Marshall, 1993) that attentional abilities are disrupted in parietal patients.

Finally, JS showed the most severe difficulties in recognizing biological motion although his low-level motion perception was intact. His lesion in the left hemisphere includes portions of the parietal lobe that has been demonstrated by fMRI studies to be involved with perception of meaningful body movement (Bonda, Petrides, Ostry, & Evans, 1996). Further fMRI studies have confirmed this notion (Grèzes et al., 2001) and showed that the left intraparietal cortex is involved in the perception of non-rigid biological motion. Perception of biological motion plays an important role in identifying and interpreting the actions of others and neuropsychological studies of patients with left posterior cortical lesions have shown severe deficits in the comprehension of goal-directed reaching (Fisk & Goodale, 1988). This might suggest why our left hemipshere patient presented a more severe deficit than the right hemisphere patients. Neurophysiological (Oram & Perrett, 1994) and fMRI studies (Grossman et al., 2000) all point to the existence of a mechanism in the brain specialized for perception of biological motion which most likely lies outside the classical motion routes that includes V5 area and, our patients' performance is in agreement with this claim.

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