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Pure agnosia for mirror stimuli after right inferior parietal lesion

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Summary

This study reports the experimental investigation of G.R., a patient suffering from a highly specific disorder in discriminating mirror stimuli following a right temporoparietal cerebrovascular accident. G.R. showed intact perceptual, attentional, mnestic, linguistic and executive abilities. Object recognition was accurate even under unusual viewing conditions. He was highly accurate in defining the canonical orientation of common objects and in discriminating misoriented objects among identical distracters. However, he was severely impaired in tasks requiring mirror-stimulus discrimination, a deficit that persisted even when the object's coordinates were systematically misaligned with respect to his body. The disorder was also dependent upon the frame of reference (allocentric versus egocentric) activated on the basis of task demands. These results demonstrate the existence of a highly specific disorder in discriminating mirror stimuli defined in object-based coordinates, suggesting a failure in processing the directionality of an object's intrinsic *x*-axis.

Keywords: mirror images; object recognition; frames of reference; agnosia

Abbreviations: BORB = Birmingham Object Recognition Battery; VOSP = Visual Object and Space Perception test

Introduction

An intriguing neuropsychological finding in the domain of visual perception is that object recognition and the processing of object orientation are supported by different brain mechanisms. Friedrich Best was the first to describe striking difficulties in judging object orientation and preserved object recognition, in a patient who suffered bilateral lesions to the inferior parietal regions (Ferber *et al*., 2003).

The same pattern has been described recently in other patients (Turnbull *et al*., 1997*a*; Turnbull, 1997; Karnath *et al*., 2000; Cooper and Humphreys, 2000; Harris *et al*., 2001). They show difficulty in judging whether an object is presented in its upright everyday-life orientation or misoriented. Some patients may copy line drawings accurately yet systematically ignore the orientation of the original, 'normalizing' misoriented drawings to their upright orientation (Turnbull *et al*., 1995; Solms *et al*., 1998). At least one case showed the converse dissociation: Patient D.M. (Turnbull, 1997) correctly defined the orientation of the majority of the objects he could not recognize. Finally, some patients can recognize letters effortlessly despite lacking information regarding their orientation (Solms *et al*., 1988; Robertson *et al*., 1997).

Other dissociations have been observed within the domain of object orientation processing. Patients may show difficulty in detecting targets rotated 180° clockwise with respect to upright distracters (Turnbull *et al*., 1997*a*; Harris *et al*., 2001). At least in one case (Patient S.C.; Turnbull *et al*., 1997*a*), discrimination of drawings rotated 180° clockwise was impaired (29 correct out of 50), whereas mirror-stimulus discrimination was spared (50 out of 50). The converse pattern of impaired mirror-stimulus discrimination with spared discrimination of other orientations has also been reported. Patients R.J. (Turnbull and McCarthy, 1996) and F.I.M. (Davidoff and Warrington, 2001) had severe difficulty discriminating mirror stimuli. However, their performance was largely spared in discriminating other stimulus rotations (e.g. 45°, 90° and 180° clockwise). Moreover, object recognition, at least for objects observed from conventional canonical viewpoints, was intact. These results suggest that mirror-stimulus discrimination and processing of other object rotations (e.g. 180° clockwise) might be subserved by relatively independent brain systems.

Various theoretical accounts have been proposed to explain the disorder for mirror stimuli. Turnbull and McCarthy

(1996) suggested that it might be due to an inability to assign suitable frames of reference to the observer's body (egocentric coordinates), to the inspected object (allocentric coordinates) or to a translation from allocentric to egocentric coordinates. R.J. had difficulty judging stimulus orientation with reference to a leftward or rightward arrow, suggesting impairment of handedness encoding. Unfortunately, this hypothesis could not be tested. Harris and colleagues have recently advanced a similar hypothesis to explain orientation agnosia as a deficit in finding coordinate axes (Harris *et al.*, 2001).

Davidoff and Warrington (2001) have proposed an explanation of mirror-stimulus discrimination deficit in terms of pathological engaging on viewer-independent representations supported by the posterior inferotemporal cortex (i.e. the ventral visual pathway; Ungerleider and Mishkin, 1982; Milner and Goodale, 1995). At least for objects viewed from angles in which critical features are available to the observer, viewer-independent representations might be the principal gateway for object recognition, identification and naming (Davidoff and Warrington, 1999; Warrington and Davidoff, 2000). Microelectrode single-cell recordings from area IT in monkeys have shown invariant responses for original and mirror stimuli (Rollenhagen and Olson, 2000; Baylis and Driver, 2001), suggesting a representational format that is independent of object orientation. The spatial attributes of objects, however, would be coded by viewer-dependent mechanisms supported by parietal networks (i.e. the dorsal pathway; Ungerleider and Mishkin, 1982; Milner and Goodale, 1995). Viewer-dependent representations are sensitive to orientation changes relative to the observer and would subserve object recognition under non-optimal viewing conditions (e.g. when objects are fragmented, overlapping, shaded or foreshortened; for review see Turnbull *et al.*, 1997*b*). Thus, if, after parietal damage, object processing takes place only in the ventral pathway, the engagement in viewer-independent representations might prevent accurate analysis of object orientation, leading to confusion of mirror stimuli.

In support of this hypothesis, Warrington and Davidoff (2000) reported the case of Patient J.B.A., who presented with severe difficulty in both object recognition and mirror discrimination tasks. J.B.A.'s performance in mirror discrimination tasks was markedly better for objects that she was not able to recognize. Warrington and Davidoff (2000) explained the improvement in mirror-stimulus discrimination as a consequence of disengagement from these viewer-independent representations. Furthermore, Patient F.I.M. (Davidoff and Warrington, 2001), who showed a deficit in discriminating mirror stimuli, was markedly impaired in recognizing objects observed from unusual viewpoints, but was very accurate with the same objects when viewed from conventional, canonical viewpoints, in which critical features can be processed easily. The association between agnosia for unusual views and impaired discrimination of mirror stimuli was taken to support the engagement hypothesis. Note that Patient R.J. (Turnbull and McCarthy, 1996) also had considerable difficulty recognizing silhouettes and objects observed from unusual viewpoints, despite intact object recognition under normal viewing conditions. In summary, these studies seem to indicate competition between viewer-dependent and viewer-independent mechanisms. As a consequence, engagement of the viewer-independent mechanism would cause mirror discrimination impairment, with object recognition preserved except for the case of unusual viewing conditions.

The aim of the present study was to describe a new case with a severe and highly specific impairment restricted to tasks requiring discrimination of mirror stimuli. Experiments 1–5 aimed to verify the specificity of the deficit with respect to other orientation manipulations, whereas the aim of Experiments 6–9 was to test the different explanations proposed for the mirror-stimulus discrimination deficit.

Case presentation

G.R., a 72-year-old right-handed grocer with 8 years of formal education, suffered from a right hemisphere cerebral vascular accident in December 1993. Standard neurological assessment demonstrated left hemiplegia and hemianaesthesia. Doppler echography showed a thrombotic obstruction of the right internal carotid artery and stenosis of the left internal carotid artery. A computed tomography (CT) scan evidenced a hypodense region in the right hemisphere extending from the insula to the inferoparietal region. Midline structures were not changed. Older asymptomatic lesions were present in the left inferior occipitotemporal cortex and in the cerebellum bilaterally. Functional imaging by SPECT (single photon emission computed tomography) (May, 1994) demonstrated right temporoparietal hypoperfusion. R.G. underwent a right STA-MCA (superficial temporal artery-middle cerebral artery) artery bypass operation, followed by a second operation (May, 1995) to reconstruct the left internal carotid artery.

A CT scan (January, 1996) did not reveal postoperative complications and reconfirmed the hypodense area in the right insula, extending to the corresponding subcortical white matter, combined with dilatation of the lateral ventricular structures. In May 1998 regional cerebral blood flow (rCBF) was assessed by xenon 133 clearance inhalation, demonstrating bilateral diffuse hypoperfusion, more evident in the right parietal cortex (Fig. 1). A recent MRI brain scan (March 2002), reconfirmed all previous neuroradiological findings (Fig. 1). At the time of writing, G.R.'s left hemiplegia has regressed to a moderate left hemiparesis, more evident in the left inferior limb.

Neuropsychological assessment

Following his cerebrovascular accident, G.R. presented with symptoms of left visuospatial neglect that recovered spontaneously and were completely absent during the formal neuropsychological evaluation and experimental investiga-

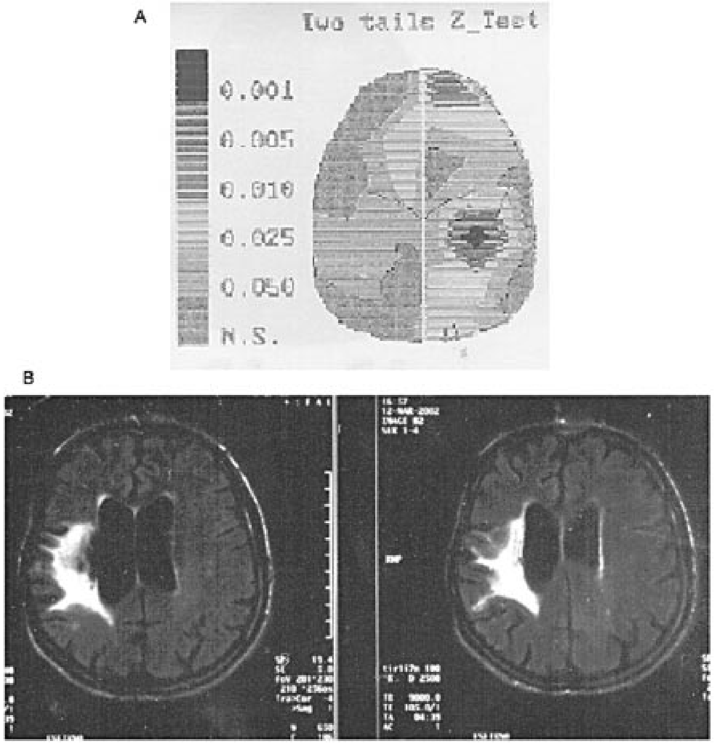

Fig. 1 (**A**) rCBF scan showing right parietal hypoperfusion. (**B**) MRI scans of G.R.'s brain. The right hemisphere corresponds to the left half of each scan.

tions. Consent for our study was obtained according to the Declaration of Helsinki. G.R. appeared alert, collaborative and fully oriented for time, space and personal information. He had no difficulties of memory or communication in everyday life and his social behaviour and emotional control remained appropriate and well adapted. Standard neuropsychological testing revealed markedly preserved perceptual, ideomotor, linguistic, memory and executive functions, adjusted for his age and educational level (Table 1).

G.R.'s perceptual abilities were well preserved both in tasks demanding feature integration (Street Completion Test) and in tasks requiring coding of critical features [Silhouettes and Birmingham Object Recognition Battery (BORB) subtest 7] or the definition of principal axes of elongation (BORB subtest 8). Thus, in contrast with Patients R.J. (Turnbull and McCarthy, 1996) and F.I.M. (Davidoff and Warrington, 2001), G.R. demonstrated well-preserved perceptual processing for both usual and unusual viewpoints. This finding appears crucial in relation to Davidoff and Warrington's (2001) viewer-independent engagement hypothesis (see General discussion).

G.R.'s constructional praxis was preserved and he displayed normal local–global attentional shifting in copying letters composed of smaller letters. Perception of symmetry was intact. In a modified version of the Benton Line Orientation Test, G.R. was presented with 16 pairs of vertically oriented lines and 16 pairs of horizontally oriented lines. Four line pairs were parallel, whereas the remaining line pairs formed angles between 5° and 15°. G.R.'s task was to judge if the lines were parallel or formed an angle. His performance was perfect for parallel (8 out of 8) and 15° (8 out of 8). He made two errors in discriminating differences of 10° (6 out of 8) and was impaired in discriminating differences of 5° (0 out of 8). Thus, G.R.'s ability to discriminate angle variations was largely spared, at least for lines that were parallel or formed angles of >5°. Furthermore, G.R. was perfectly accurate in judging lines as horizontal or vertical, suggesting intact assignment of fundamental spatial axes of reference, at least with respect to his own body.

G.R. was accurate in detecting the odd one out among four drawings in which the target could differ from the distracters in size, colour or structure or was rotated 180° clockwise, whereas he was severely impaired when it was a mirror stimulus (Table 2). This prompted the experimental investigation.

Experiment 1: orientation judgement

Introduction

Some patients (Turnbull 1997; Turnbull *et al*., 1997*a*; Karnath *et al*., 2000; Cooper and Humphreys, 2000; Harris *et al*., 2001) have difficulty deciding whether an object is presented in its upright canonical position or rotated. According to Turnbull and colleagues, they are orientation agnosics (Turnbull *et al*., 1997*a*, *b*). The aim of the present

Table 1 *Neuropsychological assessment*

	G.R.'s score (correct)	Cut-off score
Screening		
Mini-Mental State Examination (Mondini *et al*., 2001)	28/30	24/30
Attention and executive functions		
Trail-making test (Mondini *et al*., 2001)		
Form A	189 s	⩾209 s
Form B	428 s	⩾558 s
Form BA	239 s	⩾384 s
Cognitive estimation (Mondini *et al*., 2001)	4.5 out of 5	⩽3/5
Phonemic fluency (Mondini *et al*., 2001)	7.6	⩽7.3
Verbal reasoning (Mondini *et al*., 2001)	6/6	⩽1/6
Raven (short form) (Mondini *et al*., 2001)	3/12	0/12
Language		
Token test (Spinnler and Tognoni, 1987)	35/36	⩽26/36
Perceptual and spatial functions		
Street Completion Test (Spinnler and Tognoni, 1987)	7.25/14	⩽2/14
Silhouettes (Warrington and James, 1986)	19/20	–
BORB subtest 7 (Riddoch and Humphreys, 1993)	24/25	19/25
BORB subtest 8 (Riddoch and Humphreys, 1993)	23/25	19/25
Line bisection (Wilson *et al*., 1987)	9/9	⩽7/9
Letter cancellation (Wilson *et al*., 1987)	40/40	⩽32/40
VOSP, dot counting (Warrington and James, 1991)	9/10	⩽8/10
VOSP, position discrimination (Warrington and James, 1991)	20/20	⩽18/20
VOSP, number location (Warrington and James, 1991)	8/10	⩽7/10
VOSP, cube analysis (Warrington and James, 1991)	10/10	⩽6/10
Ideomotor and constructional functions		
Constructional praxis (Spinnler and Tognoni, 1987)	13/14	⩽7.75
Ideomotor praxis (Mondini *et al*., 2001)	6/6	⩽5
Memory		
Digit span (Mondini *et al*., 2001)	4	⩽3.3
Prose memory (Mondini *et al*., 2001):		
Immediate recall	13/28	⩽6.3
Delayed recall	19/28	⩽5.9
Total	16/28	⩽6.25
Corsi span (Spinnler and Tognoni, 1987)	4	⩽3.50
Corsi supraspan (Spinnler and Tognoni, 1987)	8.85	⩽5.50
Semantic memory questionnaire (Laiacona *et al*., 1993)	458/469	⩽447

experiment was to rule out the presence of orientation agnosia.

Stimuli, apparatus and procedure

Thirty-two object drawings (Snodgrass and Vanderwart, 1980) previously used by Turnbull and colleagues (Turnbull *et al*., 1997*a*) were presented to G.R. printed on a 10 × 12 cm flash card. All stimuli had a canonical, everyday-life orientation. Eight were presented at 0° (canonical orientation), eight were rotated 90° clockwise, eight were rotated 90° anticlockwise, and the remaining eight stimuli were rotated 180° clockwise. G.R. had to name the drawings and judge if they were represented in their everyday-life orientation.

Results

G.R. named every drawing correctly and was accurate in judging if the objects depicted were in upright canonical orientation or were disoriented (32 out of 32). Thus, G.R. could accurately create a viewer-centred representation and associate it with a more abstract viewer-independent representation, which specifies canonical object orientation.

Experiment 2: disoriented drawings

Introduction

The aim was to compare G.R.'s performance with that of other patients, who could copy object and non-object drawings accurately but produced systematically disoriented copies, suggesting preserved perception of object structure with impaired processing of object orientation (Turnbull *et al*., 1995; Solms *et al*., 1998).

Methods

Stimuli, apparatus and procedure

Twelve drawings depicting real objects (Snodgrass and Vanderwart, 1980), previously used by Turnbull and colleagues (Turnbull *et al*., 1997*a*), were presented to G.R.

Table 2 *Preliminary assessment of G.R. on odd one out of four drawings*

Condition	Correct
Colour	8/8
Size	7/8
Structure	6/8
180°	6/8
Mirror stimuli	1/8

printed on individual flash cards. Four drawings were presented at 0° (canonical orientation), four at 90°, four at 180° and four at 270° clockwise. G.R. was asked to copy the stimuli, respecting their orientation.

Results

G.R.'s copies were accurate and well organized, respecting both the global shape and the internal feature organization of the stimuli (Fig. 2). More importantly, the overall orientation of G.R.'s copies was well aligned with the corresponding models. There was no evidence of copy rotations. These results further confirmed G.R.'s ability to create and reproduce correct viewer-centred representations.

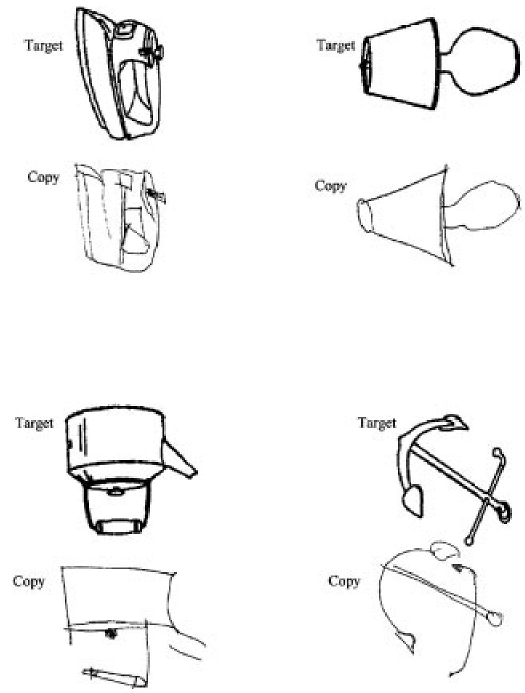

Fig. 2 G.R.'s copies of disoriented drawings.

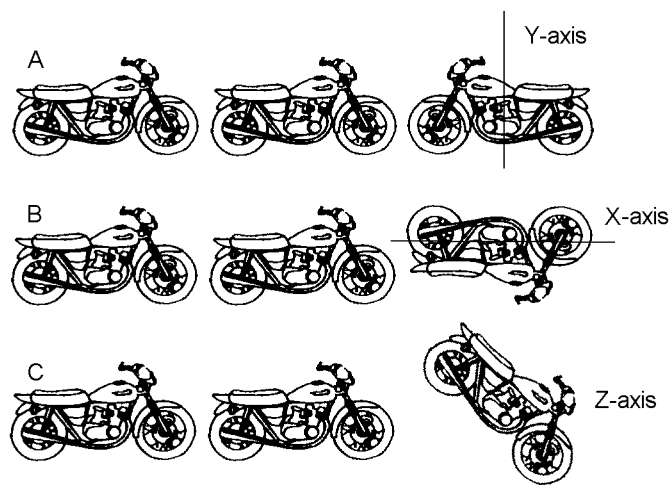

Fig. 3 (**A**) Mirror condition. (**B**) 180° (upside-down) condition. (**C**) 45° condition.

Experiment 3: discrimination of mirror stimuli

Introduction

The aim was to investigate G.R.'s difficulties with mirror images using the same procedure (odd-one-out task) and stimuli as those originally employed by Turnbull and colleagues (Turnbull *et al.*, 1997*a*).

Methods

Stimuli, apparatus and procedure

A set of five black and white drawings (Snodgrass and Vanderwart, 1980) was selected (living things: camel, bear; non-living things: piano, shoe, motorcycle). G.R. was presented with 90 trials (45 critical and 45 control trials). Each critical trial included three drawings of the same object, horizontally aligned one next to the other (Fig. 3A). Two of the stimuli had the same orientation (distracters), whereas the third stimulus was their mirror image (the odd one out). The mirror image resulted from the rotation of the object around its vertical axis (*y*-axis). Such manipulation defines directional changes along the horizontal axis (*x*-axis). Mirror stimuli appeared with the same frequency in every position and each critical trial was presented three times, giving a total of 45 trials (5 objects × 3 presentations × 3 positions). Control trials were constructed using the same set of stimuli, but the three drawings had the same orientation.

The stimuli of each trial appeared in the centre of an 18 inch PC monitor in pseudorandom order. G.R. sat ~40 cm from the monitor. His task was to name the stimuli and detect the presence or absence of the odd one out. There was no time limit and G.R. was free to move his eyes. The same task was also administered to three healthy control subjects matched for age and education (mean age 75.3 years, 8 years of education).

Results

G.R. named all stimuli without hesitation. His performance was perfect on control trials (45 out of 45), whereas it was impaired when discrimination of mirror images was required

(29 out of 45). The comparison between control and critical trials was significant [$\chi^2(1) = 17.10$, $P < 0.001$]. Performance of the control subjects was fast and errorless (control trials, 45 out of 45; critical trials, 45 out of 45). G.R. did not produce random responses, nor did he produce false alarms on control trials, showing that his errors resulted from a failure in discriminating mirror stimuli.

Experiment 4: 180° upside-down discrimination

Introduction

This experiment investigated G.R.'s ability to discriminate inverted stimuli. Turnbull and colleagues described patients with difficulties in discriminating stimuli rotated 180° clockwise (Turnbull *et al*., 1997*a*). In the present experiment, stimuli were rotated 180° upside-down instead of 180° clockwise. An upside-down rotation of 180° is a more stringent test than a clockwise rotation of 180° (Turnbull and McCarthy, 1996; Davidoff and Warrington, 2001), because the latter requires 180° rotation around the horizontal axis followed by 180° rotation around the vertical axis. Moreover, the same spatial transformation can be achieved by a clockwise rotation around the object's perpendicular axis (z-axis). The specific effect of rotation around the x-axis was tested in the present experiment, whereas the effect of rotation around the z-axis was tested in Experiment 5.

Methods

Stimuli, apparatus and procedure

These were the same as in Experiment 3, except that the odd-one-out stimulus was rotated 180° upside-down with respect to its horizontal axis (Fig. 3B).

Results

G.R. named correctly every stimulus (90 out of 90), produced only one error on critical trials (44 out of 45) and was errorless on control trials (45 out of 45). The difference in accuracy between critical trials in Experiments 1 and 2 was significant [$\chi^2(1) = 14.21$, $P < 0.001$]. Control subjects made no errors.

Thus, G.R. had spared abilities in discriminating 180° upside-down inversions (i.e. object rotation around the x-axis leading to directional changes along the y-axis), which is at odds with his impaired performance in discriminating mirror stimuli (i.e. object rotation around the y-axis leading to directional changes along the x-axis).

Experiment 5: 45° and 225° clockwise rotation

Introduction

The aim was to clarify whether G.R.'s unimpaired performance in Experiment 4 for 180° upside-down stimuli would extend to stimuli rotated around the z-axis, perpendicular to the drawing plane (i.e. picture plane clockwise rotations).

Methods

Stimuli, apparatus and procedure

These were the same as in Experiment 3, except that the odd-one-out stimulus appeared in half of the trials rotated 45° clockwise and 225° clockwise in the other half (Fig. 3C), giving a total of 60 critical trials.

Results

G.R.'s performance was accurate on both critical (59 out of 60) and control (60 out of 60) trials. The comparison between critical trials in Experiments 3 and 5 was significant [$\chi^2(1) = 19.33$, $P < 0.001$], whereas the comparison between Experiments 4 and 5 was not. Thus, G.R. had intact discrimination for stimuli rotated 45° and 255° clockwise (orientation changes along the z-axis).

Discussion of Experiments 1–5

The presence of a specific disorder regarding mirror-stimulus discrimination was confirmed by comparing G.R.'s performance in a variety of tasks. G.R.'s deficit is clearly at odds with his intact performance in both spatial (orientation judgement, copying disoriented objects, 180° upside-down rotation, and 45° and 225° clockwise rotations) and perceptual (size, shape and colour discrimination, feature integration, and recognition) tasks. Our findings replicate the previous studies by Turnbull and McCarthy (1996) and Davidoff and Warrington (2001). The aim of the following set of experiments was to establish the specific contribution of different coordinate systems of reference.

Experiment 6: egocentric versus allocentric coordinate frames of reference

Introduction

One possible explanation of the deficit for mirror stimuli is the impairment in processing coordinate frames of reference (Turnbull and McCarthy, 1996; Harris *et al*., 2001). G.R. might have specific difficulties in defining the direction of a stimulus with reference to its horizontal elongation axis (e.g. distinguishing left from right). This, in turn, might render the discrimination of mirror stimuli hard or altogether impossible, given that they differ with reference to their horizontal (x) axis. For instance, the only difference between the two mirror camels was that they were looking in opposite directions along the x-axis.

An observer can use two types of coordinates to define the horizontal x-axis of an object: egocentric coordinates and allocentric coordinates (Fig. 4). Egocentric coordinates define spatial parameters centred on the observer's body parts (e.g.

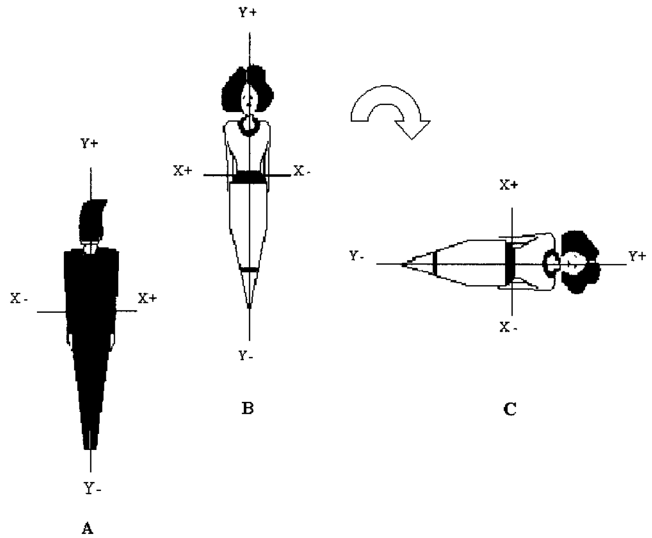

Fig. 4 (**A**) Egocentric coordinates. (**B** and **C**) Allocentric coordinates.

gaze, head, trunk, limbs) and/or between the observer's body and objects in the surrounding. Allocentric coordinates define relations within and between objects around the observer. If mirror-stimulus discrimination depends on egocentric co-ordinates, performance in tasks having as their reference G.R.'s body might be impaired. In contrast, if mirror-stimulus discrimination is a function of allocentric coordinates, G.R. might have difficulty with tasks requiring the processing of coordinates centred on objects or people in his environment. This was tested in the present experiment.

Method

G.R. and the experimenter sat facing each other. Two conditions were created to test verbal and non-verbal output. In the naming condition, G.R. was asked to name body parts indicated by the experimenter (24 trials); in the pointing condition, G.R. was asked to point to body parts named by the experimenter (24 trials). In each condition, for half of the trials the target was G.R.'s body [e.g. 'point to your left arm' (egocentric coordinates)] and for half of the trials the target was the experimenter's body [e.g. 'point to my left arm' (allocentric coordinates)]. Trials were presented in random order. For pointing, G.R. used his right, non-paretic arm.

Results

G.R. was errorless on trials based on his body (24 out of 24), but at chance level on trials based on the experimenter's body [12 out of 24, $\chi^2(1) = 16$, $P < 0.001$]. G.R. made the same number of errors in the naming and pointing conditions, demonstrating that his performance was not affected by misuse of verbal labels (right–left). As a follow-up test, a version of Piaget's 'three mountains' task (Piaget and Inhelder, 1956) was administered to G.R. He viewed an arrangement of three familiar objects and a set of four drawings depicting the scene from four different viewpoints. Remaining in one position, he had to select the drawing that would reflect how the scene would look from other perspectives in the room. He was impaired for viewpoints different from his own (50% errors).

Thus, G.R. demonstrated intact assignment of the egocentric coordinate frame (G.R.'s body or his own viewpoint) but he was severely impaired when the same trials were centred on an allocentric coordinate frame (experimenter's body or viewpoints other than his own). Although these results might not reflect a causal link with the mirror discrimination deficit, one should note that both impaired tasks involved discrimination of directional changes along the horizontal x-axis. However, one patient showing impaired mirror-stimulus discrimination (R.K., Davidoff and Warrington, 1999), in association with object agnosia and impaired space perception, had no difficulty in indicating left and right with reference to both his and the examiner's body.

Experiment 7: discrimination of vertically aligned mirror stimuli

Introduction

Experiment 7 was designed to contrast egocentric and allocentric coordinates in the context of mirror-stimulus discrimination. To disalign the two coordinate systems, the triplets of stimuli employed in Experiments 3 and 4 were displayed rotated 90° clockwise. In this way, both axes (x and y) were disaligned with respect to G.R.'s axes (note that the y-axis was still aligned in Experiment 6).

This experiment also allowed us to address a possible objection to the previous experiments. Since most stimuli were derived from objects with a clearly defined canonical upright orientation, canonical object representations could facilitate discrimination of the odd-one-out stimulus in 45°, 225° and 180° upside-down conditions. This was not the case for the mirror-stimulus condition, in which the orientation of the odd-one-out stimulus remained canonical despite rotation around the vertical axis. If G.R. ignores information regarding stimulus orientation and bases his judgements upon violations of canonical representations, his performance should be impaired in both mirror and upside-down conditions as a result of the rotation of the whole triplet of drawings.

Methods

Stimuli, apparatus and procedure

The same stimuli as those used in Experiments 3 and 4 were presented to G.R., but each triplet was rotated 90° clockwise. Thus, stimuli now appeared one below the other in a vertical arrangement. The mirror (Fig. 5A) and upside-down (Fig. 5B) conditions were presented in separate sessions. Trial sequence, apparatus and procedure were the same as in

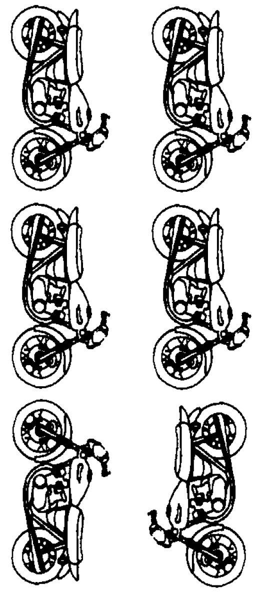

Fig. 5 (**A**) Mirror condition, obtained by 90° clockwise rotation of the triplets of Experiment 3. (**B**) 180° (upside-down) condition, obtained by 90° clockwise rotation of the triplets of Experiment 4.

Experiment 3. The task was also administered to the three healthy control subjects.

Results
In the mirror condition, G.R. made only one error on control trials (44 out of 45) but was impaired on critical trials [31 correct out of 45, $\chi^2(1) = 13.5$, $P < 0.001$). In the upside-down condition, G.R.'s performance was perfect on control trials (45 out of 45) and very accurate on critical trials (41 out of 45). The difference between critical trials in the two conditions was highly significant [31 out of 45 versus 41 out of 45, $\chi^2(1) = 13.5$, $P < 0.001$]. Control subjects made no errors.

Discussion
G.R.'s performance was unaffected by manipulations of the overall orientation of the stimulus array. G.R. was severely impaired in discriminating mirror stimuli even though they were presented vertically. Clearly, G.R. had severe difficulties in representing changes along an object's intrinsic *x*-axis when they resulted from the rotation around the object's intrinsic *y*-axis. This would happen regardless of the relationship between the object's coordinates and G.R.'s egocentric coordinates. Indeed, to achieve orientation discrimination in odd-one-out tasks, G.R. had to code differences between stimuli in each triplet (allocentric coordinates) without any reference to his own body (egocentric coordinates). G.R.'s deficit could not be attributed to defective use of verbal spatial terms (left–right), given that mirror stimuli differed along the up–down and not along the left–right axis.

The alternative hypothesis—that G.R. was using a strategy based on violation of canonical representations—was also addressed in this experiment. If G.R. were using canonical orientation information, one should expect that the 90° clockwise rotation of the triplets would render access to canonical representations equally difficult for all conditions. However, G.R. was still impaired with mirror stimuli and unimpaired with 180° upside-down stimuli, demonstrating that the use of canonical orientation information cannot account for his deficit. Nevertheless, such a strategy might be used when stimuli are canonical with reference to all axes (e.g. letters). This hypothesis was tested in the next experiment.

Experiment 8: mirror-letter discrimination
Introduction
Some stimuli, such as letters, words, and some flags, have highly canonical orientations and their mirror versions are virtually never experienced. Thus, a mirror letter might strongly violate its canonical representation (Caramazza and Hillis, 1990), whereas a mirror piano, for example, does not. In the case of mirror letters the violation of canonical representations might assist G.R. in mirror discrimination tasks.

Methods
Stimuli, apparatus and procedure
They were the same as in Experiment 3, with the exception that five upper-case letters (B, E, F, G, R) were used to construct the triplets. For each triplet, two of three identical letters had the same orientation, whereas the third was their mirror image. Mirror letters appeared twice in every position, giving a total of 30 critical trials. Thirty control trials were constructed using the same letters.

Results
G.R. was accurate on both critical (30 out of 30) and control (30 out of 30) trials. His markedly improved performance in the mirror-letters condition may indicate the possible use of cues deriving from the violation of strongly canonical letter representations, bypassing his deficit for mirror-stimulus discrimination. These results confirm previous studies involving discrimination of mirror words (Turnbull and McCarthy, 1996) and mirror letters (Davidoff and Warrington, 2001).

Experiment 9: mirror-stimulus discrimination versus virtual grasping
Introduction
It has been proposed that there are distinct brain systems for object recognition (occipito-inferotemporal, ventral pathway)

and for object localization/action (occipito-parietal, dorsal pathway) (Ungerleider and Mishkin, 1982; Milner and Goodale, 1995). The ventral system would be viewer-independent and would permit object recognition regardless of brightness, size, distance, location and orientation of the stimuli. The dorsal system, however, has a reaching component that is egocentric and a grasping component that adapts hand (egocentric) coordinates to stimulus-centred coordinates. Patients with lesions of inferior occipito-temporal regions have marked object recognition difficulties but intact object localization, whereas patients with damage to the occipitoparietal regions have severe difficulty localizing and reaching for objects (optic ataxia) but demonstrate preserved object recognition (for review see Ellis and Young, 1996).

The aim of the last experiment was to investigate if G.R. was influenced by task demands, searching for possible dissociations between tasks requiring mirror-image discrimination and tasks requiring object-grasping judgement.

Methods

Stimuli, apparatus and procedure

Triplets of stimuli, printed on the centre of A4 pages, were constructed using coloured drawings of a knife and a cup (Fig. 6). Twenty-four critical and 24 control trials were presented to G.R. The procedure was identical to Experiment 3 for the mirror-stimulus discrimination condition. In the virtual grasping condition, the same trials were presented and on each trial G.R. was asked to indicate which of the depicted objects could be grasped easily with his right hand. Although not explicitly stated, these stimuli had the handle pointing to G.R.'s right side.

Results

G.R.'s performance in discriminating mirror stimuli was perfect on control trials (24 out of 24) but remained significantly impaired on critical trials [15 out of 24, $\chi^2(1) = 11.07$, $P < 0.002$]. In contrast, G.R. was highly accurate in selecting the correct object to be grasped using his right hand (critical trials, 22 out of 24; control trials, 24 out of 24). The difference between critical trials in mirror-stimulus and grasping conditions was significant [15 out of 24 versus 22 out of 24, $\chi^2(1) = 5.77$, $P < 0.02$].

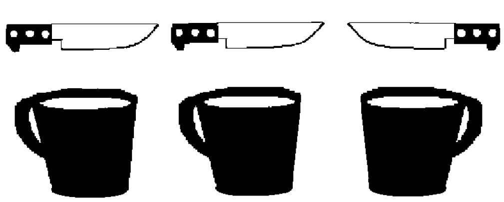

Fig. 6 Triplets of knifes and cups used in Experiment 9.

Discussion

G.R.'s performance in Experiment 9 was significantly affected by the nature of the task. Although he had difficulty discriminating between mirror stimuli, he was accurate on trials requiring virtual grasping. Note that G.R. was asked to indicate an object that could potentially be grasped without actually grasping it. This dissociation was not attributable to specific processing demands (e.g. implicit versus explicit) because in both conditions G.R. had to make an explicit, conscious judgement, guided by object orientation. Difficulties in mirror-stimulus discrimination probably reflect different underlying brain mechanisms, selectively supporting distinct coordinate systems.

Mirror-stimulus discrimination is largely based on allocentric coordinates, requiring correct detection of each stimulus and of the direction of its salient features with respect to elongation axes. Furthermore, between-stimuli comparison, an allocentric task, is required to detect the odd one out. However, grasping is based on the adaptation of the hand (egocentric coordinates) to single object structure, size and orientation, without any between-objects comparison. In order to grasp a knife, for example, it is sufficient to detect the orientation of the critical feature (the handle). If the blade is pointing to the viewer's left hand, the handle will point to the viewer's right hand (egocentric coordinates). Consequently, the right hand, being spatially compatible with the handle, will be more suitable for grasping the knife. Furthermore, during initial testing, G.R. was perfect in determining if drawings of hands presented at various angles (clockwise rotation by 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°) corresponded to his right or his left hand. During follow-up, G.R. said that his strategy was to detect the position of the thumb (critical feature) with respect to the rest of the hand and then to adapt it to his own hand. This seems to be a clear demonstration of G.R.'s intact ability to detect an object's critical features and to align his hand with them.

In short, the dissociation between mirror-stimulus processing and virtual grasping might reflect the differential involvement of allocentric versus egocentric coordinates, only the former being impaired.

General discussion

In this study we describe a patient, G.R., with severe difficulty discriminating mirror stimuli. His performance in the standard neuropsychological assessment was highly accurate. Indeed, G.R. had largely spared perceptual, attentional, mnestic, linguistic, praxic and executive functions. His normal performance in discriminating changes in colour, shape and size and on the Street Completion Test ruled out the presence of deficits at the stages of early or intermediate perceptual processing. G.R. could effortlessly judge the orientation of depicted objects (Experiment 1), make copies respecting the orientation of the model (Experiment 2), and perform odd-one-out discriminations in various orientations (Experiments 4 and 5). Thus, he showed neither orientation agnosia nor agnosia for unusual views. His spared abilities on a variety of spatial tasks not involving mirror stimuli clearly demonstrate the specificity of his deficit in discriminating mirror stimuli.

The effect of object rotation around the three main Cartesian axes, *y*, *x* and *z*, was tested in Experiments 3, 4 and 5. G.R. had difficulties only in discriminating mirror stimuli. These, in turn, were defined as the result of rotation around the object's *y*-axis, which determines reversal along the *x*-axis (Experiment 3). In contrast, G.R. was highly accurate in discriminating directional changes with reference to the *x*- and *z*-axes (Experiments 4 and 5). One might argue that the stimuli of Experiment 4 were also mirror stimuli. Davidoff and Warrington (2001), for example, have defined such stimuli as vertical mirror images. We believe this definition to be misleading. Indeed, true mirror stimuli overlap perfectly when rotated around one and only one axis of reference, whereas rotations around more than one axis were required in Experiments 4 and 5 for the odd-one-out and distracters to overlap. Thus, the odd-one-out stimuli of Experiment 3 were true mirror stimuli, whereas the odd-one-out stimuli of Experiments 4 and 5 were not.

Davidoff and Warrington (2001) hypothesized that mirror-stimulus discrimination might reflect a processing bias produced by intact, occipito-inferotemporal mechanisms subserving viewer-independent object recognition. The intact ventral pathway might prevent the damaged dorsal pathway from creating viewer-dependent representations that carry object orientation information. However, this explanation seems to be inadequate for a number of reasons.

First, if patients are engaged in orientation-insensitive representations, their performance should be impaired in every task requiring orientation judgement. Contrary to this, Patients R.J., F.I.M. and G.R. were selectively impaired only in a mirror-stimulus discrimination task, whereas their performance in tasks involving discrimination of other orientations (e.g. 45° and 180°) was largely spared. Of course, it may be argued that mirror stimuli are more difficult to discriminate. For instance, discriminating mirror letters is an extremely difficult task for 3-year-old children (Rudel and Teuber, 1963). Although this difficulty disappears during development, it might reappear in adulthood because of brain damage. An explanation in terms of task difficulty predicts that the dissociation between impaired discrimination for mirror stimuli and intact discrimination of other orientations should be observed, whereas the inverse dissociation should not. However, patient N.L. (Turnbull *et al*., 1997*a*) showed impaired discrimination for stimuli rotated 180° clockwise (29 out of 50) with errorless mirror-stimulus discrimination (50 out of 50).

Secondly, patients with a deficit of mirror-stimulus discrimination should show difficulties in perceiving objects under non-optimal viewing conditions (Warrington and Taylor, 1973; Warrington and James, 1986), which requires coding of accurate viewer-dependent representations. This was exactly the case for Patients R.J. and F.I.M., who were impaired in object recognition from unusual viewpoints, but had no difficulty recognizing an object from normal viewpoints. However, G.R. was intact in recognizing objects with hidden critical features (BORB subtest 7) or a foreshortened elongation axis (BORB subtest 8), and in copying drawings based on accurate viewer-dependent coding of models (Experiment 2). Thus, although G.R. could disengage from viewer-independent representations and create accurate viewer-dependent representations, he was still impaired in discriminating mirror stimuli. These results indicate that failure in discriminating mirror stimuli cannot be attributed to inability to disengage from viewer-independent representations.

The coordinate frame of reference hypothesis seems more plausible. According to Turnbull and colleagues, mirror discrimination difficulties might depend upon failure in assigning a suitable frame of reference to observed objects (Turnbull *et al*., 1997*a*). This frame is not necessary for object recognition but is necessary for processing orientation, including mirror-stimulus discrimination. Such a frame may be centred on egocentric coordinates, having as its reference the viewer's body, or allocentric coordinates having as their reference the intrinsic structure of the object. The role of coordinate systems was tested in Experiments 6, 7 and 9.

In Experiment 6, G.R. was perfectly accurate in naming and localizing parts of his own body (egocentric coordinates) but his performance was severely impaired when the same task was performed with reference to the experimenter's body (allocentric coordinates). In Experiment 7 the role of allocentric coordinates was further investigated by rotating 90° clockwise each triplet from Experiments 3 and 4. In Experiment 3, for example, G.R. was impaired in coding directional changes along the *x*-axis as a result of rotation around the *y*-axis, whereas he was accurate in coding directional changes along the *y*-axis after object rotation around the *x*-axis (Experiment 4). If G.R.'s performance was affected to some degree by a subtle deficit of egocentric coordinates (or of translation from egocentric to allocentric coordinates), one should expect a reversal of the deficit after 90° clockwise rotation of each triplet from Experiments 3 and 4. In other words, G.R. should be accurate in discriminating mirror stimuli and impaired in discriminating 180° upside-down stimuli. Contrary to this, G.R. was still impaired in discriminating vertically arranged mirror stimuli with respect to vertically arranged 180° upside-down stimuli. Thus, G.R.'s impairment remained clearly centred on allocentric coordinates, intrinsic to the object's structure and independent of changes with respect to his egocentric coordinates. Finally, in Experiment 9, G.R. was impaired when task execution depended on allocentric coordinates (discrimination), whereas he was accurate when task execution depended on egocentric coordinates (virtual grasping).

Within the domain of allocentric coordinates, the deficit was evident only when directional coding of the x-axis of the object was required. In contrast, G.R. was accurate in defining directional changes along other axes. We claim that the locus of the deficit is more in coding the direction of the x-axis than just in finding the x-axis (Harris *et al*., 2001). If finding the axis were the only problem, G.R. should have performed nearly at random, at least in Experiment 7. In contrast, his errors were not influenced by overall orientation modification of the triplets. These results, together with the double dissociation (Turnbull and McCarthy, 1996; Turnbull *et al*., 1997*a*) between discrimination of mirror stimuli and discrimination of other orientations, suggest further dissociations within the domain of allocentric coordinates.

The importance of the parietal region in discriminating mirror stimuli has been suggested in previous studies (Turnbull and McCarthy, 1996; Davidoff and Warrington 2001). For example, patients R.J. and F.I.M. had bilateral occipitoparietal lesions. The case of G.R. suggests a specific contribution of the right hemisphere for mirror-stimulus discrimination: his lesion was mainly in the right hemisphere, with evident hypoperfusion in the right inferior parietal region. Brain imaging studies with healthy participants should allow firmer conclusions regarding inter- and intrahemispheric localization.

In summary, our study shows the existence of a highly specific disorder in discriminating mirror stimuli in the absence of other visuospatial disorders, such as orientation agnosia or unusual-views agnosia. It is suggested that mirror-stimulus confusion depends on a failure in processing the directionality of an object's intrinsic x-axis, i.e. within an allocentric frame of reference.

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References

Baylis GC, Driver J. Shape-coding in IT cells generalizes over contrast and mirror reversal, but not figure-ground reversal. Nat Neurosci 2001; 4: 937–42.

Caramazza A, Hillis AE. Spatial representation of words in the brain implied by studies of a unilateral neglect patient. Nature 1990; 346: 267–9.

Cooper ACG, Humphreys GW. Task-specific effects of orientation information: neuropsychological evidence. Neuropsychologia 2000; 38: 1607–15.

Davidoff J, Warrington EK. The bare bones of object recognition: implications from a case of object recognition impairment. Neuropsychologia 1999; 37: 279–92.

Davidoff J, Warrington EK. A particular difficulty in discriminating between mirror images. Neuropsychologia 2001; 39: 1022–36.

Ellis AW, Young AW. Human cognitive neuropsychology. Hove (UK): Psychology Press; 1996.

Ferber S, Karnath HO. Friedrich Best's case Z. with misidentification of object orientation. In: Code C, Wallesch CW, Joanette Y, Lecours AR, editors. Classic cases in neuropsychology, Vol. II. 2nd ed. Hove (UK): Taylor and Francis. In press 2003.

Harris IM, Harris JA, Caine D. Object orientation agnosia: a failure to find the axis? J Cogn Neurosci 2001; 13: 800–12.

Karnath HO, Ferber S, Bulthoff HH. Neuronal representation of object orientation. Neuropsychologia 2000; 38: 1235–41.

Laiacona M, Barbarotto R, Trivelli C, Capitani E. Dissociazioni semantiche intercategoriali: descrizioni di una batteria standardizzata e dati normativi. Arch Psicol Neurol Psichiatr 1993; 54: 209–48.

Milner AD, Goodale MA. The visual brain in action. Oxford: Oxford University Press; 1995.

Mondini S, Vestri A, Mapelli D, Bisiacchi P. Esame Neuropsicologico Breve. Padova: LIRIPAC; 2001.

Piaget J, Inhelder B. A child's conception of space. London: Routledge & Kegan Paul; 1956.

Riddoch JM, Humphreys GW. Birmingham Object Recognition Battery. Hove (UK): Lawrence Erlbaum; 1993.

Robertson L, Treisman A, Friedman-Hill S, Grabowecky, M. The interaction of spatial and object pathways: evidence from Balint's syndrome. J Cogn Neurosci 1997; 9: 295–317.

Rollenhagen JE, Olson CR. Mirror-image confusion in single neurons of the macaque inferotemporal cortex. Science 2000; 287: 1506–8.

Rudel RG, Teuber HL. Discrimination of direction of line in children. J Comp Physiol Psychol 1963; 56: 892–8.

Snodgrass JG, Vanderwart M. A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity, and visual complexity. J Exp Psychol Hum Learn Mem 1980; 6: 174–215.

Solms M, Kaplan-Solms K, Saling M, Miller P. Inverted vision after frontal lobe disease. Cortex 1988; 24: 499–509.

Solms M, Turnbull OH, Kaplan-Solms K, Miller P. Rotated drawing: the range of performance and anatomical correlates in a series of 16 patients. Brain Cogn 1998; 38: 358–68.

Spinnler H, Tognoni G. Standardizzazione e taratura Italiana di test neuropsicologici. Ital J Neurol Sci 1987; 6 Suppl 8: 1–120.

Turnbull OH. A double dissociation between knowledge of object identity and object orientation. Neuropsychologia 1997; 35: 567–70.

Turnbull OH, McCarthy RA. Failure to discriminate between mirror-image objects: a case of viewpoint-independent object recognition? Neurocase 1996; 2: 63–72.

Turnbull OH, Laws KR, McCarthy RA. Object recognition without knowledge of object orientation. Cortex 1995; 31: 387–95.

Turnbull OH, Beschin N, Della Sala S. Agnosia for object orientation: implications for theories of object recognition. Neuropsychologia 1997a; 35: 153–63.

Turnbull OH, Carey DP, McCarthy RA. The neuropsychology of object constancy. J Int Neuropsychol Soc 1997b; 3: 288–98.

Ungerleider LG, Mishkin M. Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW, editors. Analysis of visual behavior. Cambridge (MA): MIT Press; 1982. p. 549–86.

Warrington EK, Davidoff J. Failure at object identification improves mirror image matching. Neuropsychologia 2000; 38: 1229–34.

Warrington EK, James M. Visual object recognition in patients with right-hemisphere lesions: axes or features? Perception 1986; 15: 355–66.

Warrington EK, James M. Visual object and space perception test. Bury St. Edmunds (UK): Thames Valley Test Company; 1991.

Warrington EK, Taylor AM. The contribution of the right parietal lobe to object recognition. Cortex 1973; 9: 152–64.

Wilson B, Cockburn J, Halligan P. Behavioural Inattention Test. Bury St. Edmunds (UK): Thames Valley Test Company, 1987.

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