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Research report

Selective deficit of mental visual imagery with intact primary visual cortex and visual perception

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ABSTRACT

There is a vigorous debate as to whether visual perception and imagery share the same neuronal networks, whether the primary visual cortex is necessarily involved in visual imagery, and whether visual imagery functions are lateralized in the brain. Two patients with brain damage from closed head injury were submitted to tests of mental imagery in the visual, tactile, auditory, gustatory, olfactory and motor domains, as well as to an extensive testing of cognitive functions. A computerized mapping procedure was used to localize the site and to assess the extent of the lesions. One patient showed pure visual mental imagery deficits in the absence of imagery deficits in other sensory domains as well as in the motor domain, while the other patient showed both visual and tactile imagery deficits. Perceptual, language, and memory deficits were conspicuously absent. Computerized analysis of the lesions showed a massive involvement of the left temporal lobe in both patients and a bilateral parietal lesion in one patient. In both patients the calcarine cortex with the primary visual area was bilaterally intact. Our study indicates that: (i) visual imagery deficits can occur independently from deficits of visual perception; (ii) visual imagery deficits can occur when the primary visual cortex is intact and (iii) the left temporal lobe plays an important role in visual mental imagery.

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1. Introduction

The definition of visual mental imagery as the process of “seeing with the mind’s eye” implies a close representational and neural relationship between visual perception and visual

imagery. Visual mental images are assumed by some to be picture-like or depictive in nature, that is representations which to a certain extent preserve the structural and spatial characteristics of the represented items. According to this assumption, retinotopically organized cortical areas such as the

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primary visual cortex can be similarly activated in a bottom-up fashion by afferent pathways during perception and in a top-down fashion by back-projections from memory stores during imagery (Kosslyn, 1987; Farah, 2001). A complete overlap between the neural bases of visual perception and those of visual imagery is, however, negated by the occurrence of neurological syndromes whereby perception is impaired and imagery is spared, or the reverse, although sparing of perception in presence of a deranged imagery is seemingly never complete (Farah, 2001; Bartolomeo, 2002). To account for such double dissociations following brain damage, models based on depictive representations have proposed that a shared system for perception and imagery may include specialized components dedicated to one or the other function (Behrmann et al., 1992). Yet other models claim that mental visual images are propositional or descriptive in nature, so that the brain does not have to re-enact a visual scene within the head in order to imagine it. According to such models mental visual images do not require that a visuotopic pattern of neural activity be conjured up at some early station along the visual pathways (Pylyshyn, 1973). These different views of mental visual imagery are the object of current vigorous debates, but whichever model one favours, the quest for the brain regions, which are involved in visual perception or visual imagery or both is obviously of general interest for clinical neurology and experimental neuropsychology alike. Evidence that is relevant to this issue comes from two main lines of research: the clinical consequences of localized brain damage and the brain patterns of activation observed during visual performances in normal subjects. According to the first line of research, damage to the occipital lobe, which contains most of the retinotopic visual areas and is essential for normal visual perception, is neither necessary nor sufficient to produce visual imagery deficits. At least with regard to object form and colour, imagery deficits are instead often observable after left temporal damage, independent of the presence or absence of conspicuous visual perceptual deficits (Bartolomeo, 2002; Luzzatti et al., 1998; Trojano and Grossi, 1994). By contrast, the second line of research has frequently, though not always, shown activations of occipital areas, down to and including the primary visual cortex, along with many extra-occipital activations, during mental visual imagery in normal subjects (Ganis et al., 2004; Mellet et al., 2000; Slotnick et al., 2005).

The present report of two patients with brain damage from closed head injury precisely localized with computerized techniques is intended to contribute to the understanding of brain lesions leading to a very clear dissociation between a normal visual perception and a severely defective visual imagery. In both patients, this dissociation has occurred in the presence of a completely intact visual cortex. Normal mental imagery in non-visual sensory domains as well as in the motor domain was found in one patient while tactile imagery deficits were found in the other.

2. Patients and method

Patient 1 is a 29-year-old, right-handed woman who works as a clerk. In 1998 she suffered a closed head injury resulting in

a hemorrhagic lesion in the middle and inferior temporal gyrus of the left hemisphere. Patient 2 is a 23-year-old, right-handed man employed as a factory worker. In a car accident in 2000 he suffered a closed head injury with brain lesions in the left temporo-occipital area and the left medial and superior parietal lobe. After the trauma both patients went into a coma (Patient 1: Glasgow Coma Scale (GCS) = 5, length of coma = 16 days; Patient 2: GCS = 3, length of coma = 14 days). When they regained consciousness, they did not present any serious somatic or motor disabilities or signs of ideomotor or ideative apraxia. Initial difficulties in verbal memory, namely in word list learning tasks, cleared up in a few months. Language was preserved, even though Patient 2 showed some anomia and alexia with intact writing. Campimetric examinations showed no visual defects in Patient 2. In Patient 1 the first campimetric examination showed patches of reduced sensitivity in the right visual hemifield, greater in the lower than the upper quadrant. These defects had disappeared 2 years after the accident, suggesting that they were most probably due to acute post-traumatic oedema. Nine months after the accident, both subjects were self-sufficient in daily activities and able to return to their jobs.

Difficulties in visual mental imagery were reported during interviews carried out 2 years (Patient 1) and 1 year (Patient 2) after the brain damage. Patient 1, for example, reported her difficulty in ordering lunch or appetizers: “When they ask me if I want some crisps or peanuts, I’m unable to answer because I can’t mentally distinguish their different shapes”. Crucially, she was perfectly able to choose among crisps or peanuts when they were presented visually. Patient 2 complained of his inability to draw when he did not have a model to copy from. It is of interest that these complaints of both patients were limited to animals and objects, but did not involve familiar faces. Recognition of faces of relatives as well as of persons encountered after the accident, such as rehabilitation staff, was apparently intact. The subjects were submitted to general neuropsychological assessments in order to ascertain the specific nature of these disorders.

2.1. Neuropsychological assessment

Each patient underwent a battery of tests assessing general cognitive abilities, language, memory, and visuo-perceptual abilities in four sessions carried out 2 years (Patient 1) and 1 year (Patient 2) after the brain injury.

General cognitive abilities were tested using the Weschler Adult Intelligence Scale-Revised (WAIS/R – Weschler, 1997) and the Raven 48 Progressive Matrices Test (Raven, 1954). Patient 1’s scores were well within the normal limits (WAIS/R: verbal = 100, performance = 95, Raven = 53/60), while Patient 2 showed a large difference between his verbal and performance scores, both of which, however, were still within the normal range (WAIS/R: verbal = 99, performance = 74, Raven = 40/60).

2.2. Language

For language assessment the Aachener Aphasia Test was utilized (Huber et al., 1991). It includes an analysis of spontaneous conversation, five subtests of comprehension (token

test, word and sentence comprehension, and comprehension of written words and sentences), five repetition tasks (repetition of sounds, words, foreign words, compound words and syntagma, sentences), four written language subtests (reading, dictation of words and sentences, and spontaneous writing) and four denomination tests (objects, colours, compound words, and description of images).

2.3. Memory

Standard tests were used to assess verbal memory (word span, verbal supra-span, story recall) and visual memory (Corsi span, long-term spatial memory) (Spinnler and Tognoni, 1987). A behavioural memory test (Wilson et al., 1990) was also used with Patient 1.

2.4. Visuo-perceptual abilities

Several clinical tests were carried out to assess the subjects' recognition of objects, faces and colours, and their ability to rotate visual stimuli mentally. The same tasks were carried out by five healthy subjects (3M/2W, mean age = 30.6 years, standard deviation – SD = 1.82) and their lowest score was considered the cut-off point. Further tests included the line orientation judgement test (Benton et al., 2000) and a modified version of the constructional apraxia test (Arrigoni and De Renzi, 1964). Perceptual and spatial abilities were further investigated in Patient 2 by means of eight tasks tapping gross shape detection, perception of objects (incomplete letters, silhouettes, object decision and progressive silhouettes), and perception of space (dot counting, position discrimination, number location and cube analysis) (Warrington and James, 1991). Spatial orienting and navigation skills, the recall of routes in familiar environments and imagining a new route following the examiner's indications were assessed. The results of these tests, which showed an essentially normal performance by the patients, are shown in Table 1 and in Section 3.

2.5. Visual mental imagery assessment

Patients were tested for their ability to recall the shape or colour of objects (for instance a guitar) or animals (for instance a giraffe). The presence of visual imagery disorders was further investigated by means of systematic tests including: (1) imagery questionnaires, (2) a drawing from memory task, and (3) a task which assesses constructional abilities driven by imagery (e.g. reconstruction of puzzles). With the imagery questionnaires, patients were asked to mentally evaluate the structural characteristics of symbols, objects and animals by classifying them according to specific demands (Policardi et al., 1996). For example, in the animal tails task and the animal legs task, the patient had to decide whether a given animal's tail, legs and ears are long or short in proportion to the body or in comparison to those of other animals. The questionnaires also include symbol imagery tasks (letters, everyday symbols, and road signs). Object tasks involved mental judgements about height and width, sharpness and roundness, thickness and thinness, topological and metrical relations within and between items, the attribution of appropriate colours to objects, and mental hue comparisons. The

Table 1 – Standardized evaluation of language, memory and visuo-spatial perception in the two patients

	Patient 1	Patient 2	Normal performance
<i>Language (A.A.T.)</i>			
Token test	0 err.	0 err.	6 err. (± 4)
Comprehension	114	116	107 (± 11)
Repetition	150	150	144 (± 8)
Written language	90	87	82 (± 7)
Denomination	105	118	106 (± 8)
<i>Visuo-perceptual abilities</i>			
			Cut-off
Object recognition (n = 12)	12	12	12
Face recognition (n = 14)	14	14	14
Colour recognition (n = 12)	12	12	12
Mental rotation of figures (n = 80)	72	73	70
Constructional apraxia (n = 12)	12	12	12
Line orientation judgement (n = 30)	27	27	24
<i>Memory</i>			
			Mean (SD)
Short-term verbal memory (word span)	4	6	4.7 (0.8)
Verbal supra-span (Buschke-Fuld)	145	108	135.3 (25.9)
Story recall	12.09	11.02	13.3 (2.6)
Short-term spatial memory span (Corsi)	5	4	5.1 (1.01)
Long-term spatial memory (Corsi)	25.89	24.99	23.2 (5.7)
Reference values from normal subjects are reported in the right-most column.			
The pathological performances are given in bold.			

performances of the patients in these tasks were compared with their performances in five other tests (big/small animals, four/two-legged animals, big/small objects, wheeled/non-wheeled vehicles, and semantically associated colours) that can be carried out successfully without making recourse to visual imagery (for example, “Are horses four-legged or two-legged?”). By comparing visual imagining and non-imagining tasks it is possible to distinguish between a genuine visual imagery disorder and a semantic memory disorder.

2.6. Non-visual imagery and perception

In order to establish the visual specificity of the patients' imagery disorders, perceptual and imagery abilities in the auditory, tactile, gustatory and olfactory domains, and in movement execution and imagery were systematically assessed. Non-visual mental imagery abilities were assessed by asking patients to select on the basis of similarity two items in each of 15–20 trios in each of the auditory, tactile, olfactory and gustatory modalities. These imagery questionnaires, except those regarding taste and olfaction, were modelled on those of a previous study (Chatterje and Southwood, 1995). An example from the 20 questions for the auditory modality is “Name the two instruments among the horn, the flute and the trumpet that are similar in sound” (expected response: “horn and trumpet”). An example from the 20

questions for the tactile modality is “Name the two items among a sweater, a blanket and a shirt that are similar in texture (feel) (expected response: “sweater and blanket”). Two examples from the 15 questions regarding taste are “Name the two items among a lemon, an orange and a grape-fruit that are similar in taste (expected response: “grape-fruit and lemon”); “Name the two items among bresaola (a sweet Italian ham), prosciutto and speck (a smoked ham) that are similar in taste (expected response: bresaola and prosciutto)”. An example from the 15 questions regarding odours is “Name the two items among onion, garlic and leek that smell in a similar way (expected response: “onion and leek”).

Perceptual abilities in non-visual modalities were assessed to rule out the presence of low-level sensory deficits. Patients were asked to recognise and name 25 noises typical of living or non-living items (e.g., a dog’s bark, the sound of a violin). Moreover, they were asked to report verbally by touch the orientation of 25 lines with different distances between ridges and grooves. The possible presence of gustatory and olfactory perceptual disorders was assessed by means of a detailed interview.

Motor abilities were assessed by requiring patients to execute sequences of actions (36 items) and to assume postures (36 items) (Smania et al., 1995). Motor imagery was assessed by asking patients to verbally describe sequences of actions (36 items) or postures (36 items) named by the examiner (Smania et al., 1995). The patients’ scores in all these tasks were compared with the performances of five healthy subjects (3M/2W, mean age = 30.6 years, SD = 1.82).

2.7. Drawing from memory and copy tasks

Patients were asked to draw a strawberry, a pear, a giraffe, a rhinoceros, and a butterfly first from memory and then by copying a model. Three judges rated the similarity of each drawing with the target object by using a Likert-like numerical scale ranging from 1 (no similarity with the model or the prototypical representation of the object to be drawn) to 7 (extremely similar to the model or the prototypical representation of the object to be drawn). The raters had no information about the type of task (from memory or from copy) or about the author of each drawing. For each drawing task, the patients’ performance was compared with that of five age- and education-matched, healthy controls by means of one-sample t-tests. For both patients and controls the performances in the two drawing tasks were compared by means of paired t-tests.

2.8. Constructional abilities

Patients were asked to carry out the reconstruction of simple black and white puzzles (three or four pieces) by copying a model or without any model. When they executed the task without a model they were using their imagery abilities, which were not required during the copying task.

2.9. Mapping of the brain lesions

Standard clinical MRI (magnetic resonance imaging) radiological prints were available for each patient. The prints were

scanned on a flatbed scanner. The reconstruction of the lesions was made by means of the Multilingual Internet Names Consortium (MINC) toolkit (<http://www.bic.mni.mcgill.ca/software>). The slices were stacked in order of acquisition and merged into a single volume. Interslice registration was performed according to slice thickness and interslices’ gap measures. Each of the reconstructed MRI brain volumes was registered into the Talairach proportional stereotaxic space using nine-parameter linear registration (Talairach and Tournoux, 1988; Economo and Koskinas, 1925). The interactive program DISPLAY (J.D. MacDonald, Brain Imaging Centre, Montreal Neurological Institute; www.bic.mni.mcgill.ca/software/Display/Display.html) was used to visualize the reconstructed brain volume. This program allows a simultaneous visualisation in 3-D of the movement of the cursor in the sagittal, axial, and coronal planes of the MRI. By using the DISPLAY ‘mouse-brush’ specific voxels can be coloured. This procedure accompanied with the 3-D view of the MRI planes allows a better identification of the lesions borders. Two raters, who ignored the identity and the clinical condition of the patients, manually segmented the voxels affected by the lesion. Once the lesion was delimited, DISPLAY sulcal patterns were used as landmarks to locate and reconstruct the lesions in terms of the Brodmann’s cytoarchitectonic maps (1909). A similar procedure has been used in a previous study (Miceli et al., 2001).

3. Results

The two patients did not show any disorders of language, memory or cognitive abilities that could be revealed by our assessments. In the language tasks both patients achieved normal scores in all the battery tests, which they carried out without any difficulties. In the memory tests both patients showed no significant impairment in either verbal or visual memory, and Patient 1’s performance (score 9/12, cut-off 8/12) in a behavioural memory task (Wilson et al., 1990) was also normal. What is more important for the present purposes is that the patients also showed no apparent impairments in their visual perceptual abilities. They performed the tasks involving the recognition of objects, faces and colours, and the mental rotation of visual stimuli, clearly within the normal range as defined in Section 2 and documented in Table 1. They also performed normally in the orientation line judgement test (Benton et al., 2000) and the modified version of the constructional apraxia test (Arrigoni and De Renzi, 1964). Patient 2’s performance in visual objects and spatial perception additional tests (see Section 2) was again normal except in the silhouette task, where his score of 12/30 was definitely below the normal cut-off of 16/30 (incomplete letters: 20 – cut-off = 17/20, object decision: 15 – cut-off = 15/20, and progressive silhouette: 14 – cut-off = 14/20). It is interesting that this test calls for visual imaginative abilities more than all the other tests in the battery (Warrington and James, 1991). Neither Patient 1 nor Patient 2 showed any difficulty in spatial orienting and navigation skills, during recall of routes and environment or in imagining a new route following the examiner’s indications.

3.1. Visual imagery

Both Patient 1 and Patient 2 reported several difficulties in tasks requiring visual imagery. In the description of objects, they dwelt upon details concerning their function, but were unable to describe their shape. For example, in the description of a guitar, Patient 2 declared: “It is a thing that you can play...you play it with one hand here and the other hand here (he moved his hands accordingly) but its shape...I don’t know”. When describing a giraffe, Patient 2 listed the single parts of the body (the head, the body, the legs, etc.) but omitted the tail and did not mention the long neck. When asked to describe an elephant, Patient 1 failed to report the trunk and tusks as characteristic body parts of that animal.

3.2. Imagery questionnaires

Table 2 shows the patients’ scores in the visual imagery questionnaires, compared to the normal performances of healthy subjects. The severely defective performances in the imagery tasks are in stark contrast with the virtually normal performances in the perceptual tasks. Further, both patients performed much worse than controls in all the subtests of the

visual imagery questionnaires, except for comparison of similar letters, animal tails and high/wide object judgement tasks, where Patient 1 performed within normal limits (see Table 2).

Table 2 also shows that both patients performed poorly in memory tasks that obligatorily required visual imagery (such as a forced-choice response indicating whether a sheep’s ears are pointing upward or downward) but not in memory tasks that could be carried out based on purely semantic knowledge, without using visual imagery (such as a forced-choice response indicating whether a horse is four-legged or not). The patients’ impaired performance on memory tasks involving visual imagery was fully manifested on tasks with forced-choice responses as well as with tasks requiring the free description from memory of, for example, road signs (Table 2), or drawing from memory (Fig. 1).

Both patients performed very well in perceptual tests assessing auditory (hits were 24/25 in Patient 1 and 25/25 in Patient 2) and tactile abilities (hits were 23/25 in Patient 1 and 25/25 in Patient 2). Further, their performance was perfect in tests tapping abilities to execute 36 sequences of actions and to maintain 36 postures.

Table 3 shows the performance of patients and controls in non-visual sensory imagery and motor imagery tasks.

Table 2 – Patients’ scores in the visual imagery questionnaires

	Patient 1	Patient 2	Normal scores mean (SD)
Visual imagery tasks			
Symbol imagery			
Straight/curved letter (n = 40)	38	36	40 (0)
Top/bottom larger letter (n = 14)	6	4	13.8 (0.64)
Comparison of similar letters (n = 14)	14	12	14 (0)
Everyday symbols (n = 20)	6	7	16.3 (1.2)
Road signs description (n = 10)	6	5	8.6 (1.14)
Animal imagery			
Comparison of paired animals (n = 30)	25	23	29.3 (0.64)
Animal ears (n = 20)	13	14	18 (1.18)
Animal legs (n = 30)	24	20	29.1 (0.94)
Animal tails (n = 20)	18	14	18.7 (1.10)
Animal visual comparison (n = 20)	10	8	17.2 (1.46)
Object imagery			
High/wide object judgement (n = 30)	30	20	29.2 (0)
Sharp/rounded object (n = 30)	23	20	28.8 (0.97)
Thickness object judgement (n = 30)	27	25	29.6 (0.66)
Object visual comparison (n = 20)	15	12	18.6 (1.01)
Topological relation within object (n = 15)	10	11	14.3 (1.18)
Metrical relation within object (n = 15)	10	11	14.2 (0.6)
Colour imagery			
Object colour judgement (n = 41)	28	27	38.5 (2.41)
Mental hue comparison (n = 20)	15	15	18.9 (1.13)
Visual non-imaginal tasks			
Big/small animal (n = 30)	30	29	30 (0)
Four-legged animal (n = 20)	20	20	20 (0)
Big/small object (n = 30)	29	29	29.3 (0.90)
Wheeled vehicles (n = 20)	18	20	19.6 (0.66)
Semantically associated colours (n = 30)	26	23	19.3 (0.78)

Reference values for healthy subjects are drawn from Policardi et al. (1996). According to the latter authors, visual non-imaginal tasks are those visual memory tasks that can be performed based on semantic knowledge, without making recourse to visual imagery.

The pathological performances are given in bold.

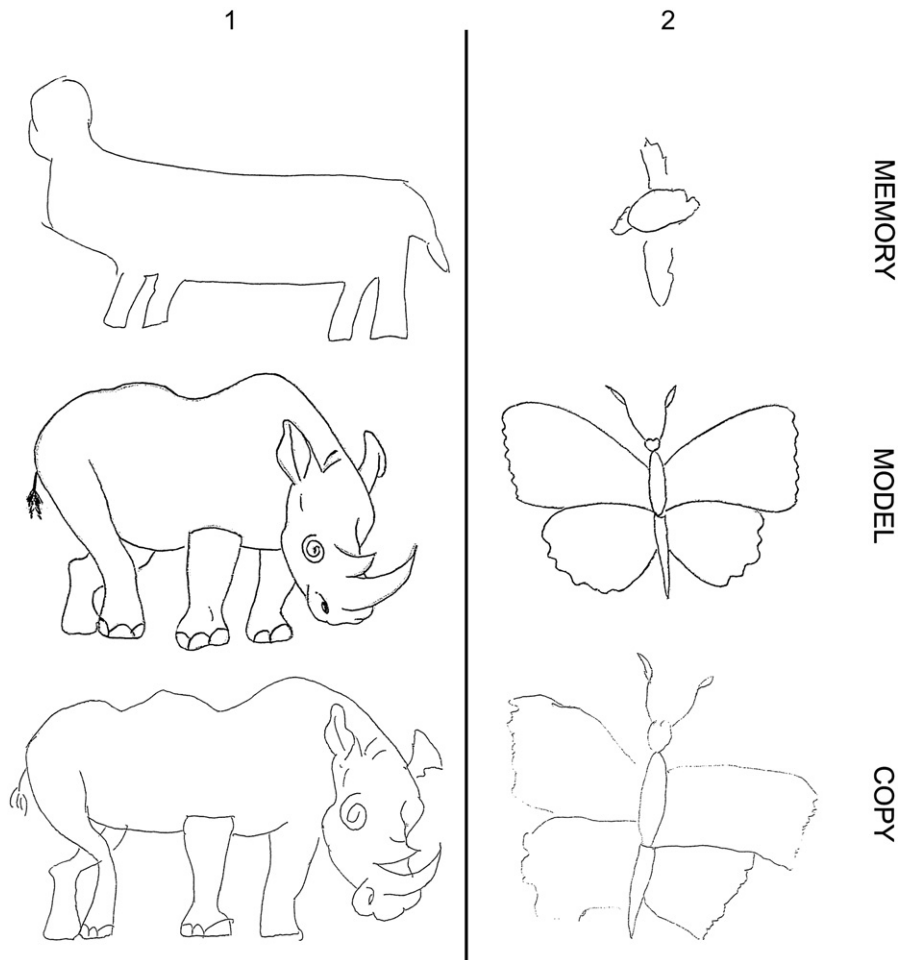


Fig. 1 – Representative drawings from memory (upper part) and from copy (lower part) in Patient 1 (left part) and Patient 2 (right part). The models to be copied are represented in the middle part of the figure.

One-sample t-tests were used to compare the performance of each patient in non-visual sensory imagery and motor imagery tasks with the scores of the control group. Results show that both patients were not different from controls in the auditory imagery task (Patient 1: $t(4) = -.23, p = .83$; Patient 2: $t(4) = 2.09, p = .105$). In the gustatory and olfactory domains Patient 1 performed even better than controls (gustatory: Patient 1 = $t(4) = -3.21, p = .033$; Patient 2 = $t(4) = -.53, p = .62$ – olfactory: Patient 1 = $t(4) = -2.89, p = .045$; Patient 2 = $t(4) = 2.27, p = .09$). In the tactile imagery task, while no difference between Patient 1 and controls was found ($t(4) = -.53, p = .62$),

Patient 2 performed much worse than controls ($t(4) = 18.17, p < .0001$). In motor sequence and posture imagery tasks patients and controls performed without errors.

3.3. Drawing from memory and copy tasks

Representative examples of drawings from memory and copy tasks for each patient are shown in Fig. 1.

The impairment in tests requiring visual imagery can be immediately gauged on the basis of the differences in quality between the drawings from memory and those from copy (see Fig. 1). Compared to the drawings from copy, the drawings from memory appear extremely poor and lacking in those details that typify each animal (e.g., the neck of a giraffe or the horn of a rhinoceros).

In the drawing from memory task, the performance of both patients was judged much worse than that of controls (Patient 1 vs C: $t(4) = 16.31, p < .0001$; Patient 2 vs C: $t(4) = 17.89, p < .0001$, one-sample t-tests). In the drawing from copy task, where visual imagery has a minor role, Patient 1 did not differ significantly from normal controls ($t(4) = 1.82, p = .143$), in contrast to Patient 2 who scored significantly worse than controls ($t(4) = 10.93, p < .0001$) (see Fig. 2). Crucially, while performance

Table 3 – Non-visual sensory and motor imagery tasks in the patients and control subjects

	Patient 1	Patient 2	Controls (SD)
Tactile (n = 20)	18	11	17.8 (0.84)
Auditory (n = 20)	17	15	16.8 (1.92)
Gustatory (n = 15)	13	12	11.8 (0.84)
Olfactory (n = 15)	15	10	12.2 (2.17)
Postures (n = 36)	36	36	36 (0)
Motor sequences (n = 36)	36	36	36 (0)

The pathological scores are given in bold.

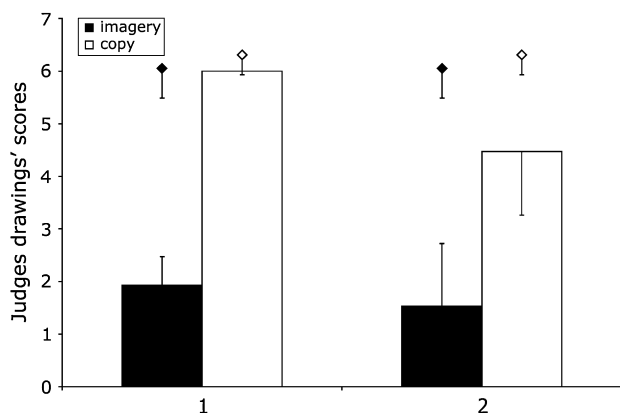


Fig. 2 – Mean (\pm standard deviation) scores of performance in drawings from memory and copy tasks for the two patients (black and white columns) and in five healthy, age- and education-matched controls (black and white diamonds). Three independent raters, unaware of the author of the drawing and of the experimental task (copy or drawing from memory), were used. Higher scores (on a 0–7 Likert scale) indicate better performance.

in the drawing from copy and drawing from memory tasks did not differ in control subjects ($t(4) = 1.33$ $p = .25$, paired t -tests), both patients performed much worse in the memory task than in the copy task (Patient 1: $t(4) = 16.58$ $p < .0001$; Patient 2: $t(4) = 3.29$ $p = .03$, paired t -tests) (see Fig. 2).

3.4. Constructional abilities

Patient 1 and Patient 2 were completely unable to construct puzzles if they did not have a model to copy. In contrast, they easily completed the task if they could see the model of the image they had to reconstruct.

3.5. Analysis of the brain lesions

The reconstruction of the lesions in the two patients is shown in Fig. 3.

Patient 1's lesion is localized in the middle and inferior temporal gyri of the left hemisphere, caudally to the temporal pole and rostrally to the temporo-occipital incisura (Fig. 3); the upper boundary almost reaches the superior temporal sulcus while ventrally includes the inferior temporal gyrus (Brodmann area (BA) 21, 20, and the ventro-rostral aspect of BA 37).

In Patient 2, one lesion is localized in the left temporo-occipital around the temporo-occipital incisura at the border among the fusiform and the inferior occipital gyri (BA 37, 19). One lesion involves the left medial parietal lobe up to the subparietal sulcus and in part the parieto-occipital sulcus (BA 7). In the left dorso-parietal region the lesion is limited to the superior parietal lobe (BA 7) (Fig. 3). A similar, but smaller lesion is present in the right parietal lobe.

4. Discussion

The results show that a conspicuous deficit of mental visual imagery can occur in the complete absence of visual agnosia,

low-level visual perceptual deficits, and memory or language disorder. A relatively selective impairment of visual imagery following some forms of brain damage, as well as dissociations between poor visual imagery and fair visual perception, has been reported in a number of previous studies (Bartolomeo, 2002; Kaski, 2002). The severely disordered ability for generating and using visual images described here is interesting in that it was displayed by two brain damaged patients with a visual system apparently enabling a largely normal visual perception and including an anatomically intact primary visual cortex (V1). Small lesions of the optic radiations as well as the possible emergence of visual perceptual deficits with more demanding tasks cannot be totally excluded. Yet it is unlikely that such minor lesions and deficits, if present, could account for the patients' severe impairment on a wide range of visual imagery tests, including tests for imagery of object shape, size and colour, letter shape, and animal parts, plus drawing from memory, all of which are thought to require the mental manipulation of visual images. Since the capacity to form mental visual images and especially to evaluate them introspectively differs widely among normal observers, it seems necessary to exclude that visual imagery might have been poor in these patients even before their closed head injury. This possibility is ruled out by the fact that it was the patients themselves who spontaneously reported a subjective loss of visual imagery and complained about it as a particularly noticeable and annoying consequence of their injury. It should also be stressed that the visual imagery impairment in these patients was seemingly restricted to an inability to generate mental visual images from semantic knowledge such as, for example, a precise dog image upon hearing or reading the word dog. The generation of visual images driven from visual inputs did not seem to be affected. The striking impairment of visual imagery in these patients can be accounted for by the evidence that the left inferior temporal gyrus (BA 37) was damaged in both of them, in keeping with previous imaging and clinical studies (Bartolomeo, 2002; Mellet et al., 2000) which have argued for a crucial, causative role of cortical temporal areas in visual imagery. However, several areas of the left hemisphere, in addition to those of the temporal lobe, are probably involved in mental imagery. It has been recently shown that the mental generation of visual images is interfered with by inhibitory stimulation of left parietal cortical areas, whereas the analysis of visual images, and more specifically the spatial comparison of the imagined content, is interfered with by inhibitory stimulation of right parietal cortical areas (Sack et al., 2005). Moreover, a predominance of the left hemisphere in the generation of non-visual mental images is suggested by the recent functional magnetic resonance imaging (fMRI) evidence that the left insula is preferentially activated by gustatory imagery tasks (Kobayashi et al., 2004). While clearly in line with the notion of a predominance of the left hemisphere in the generation of mental images, the present findings expand previous knowledge by suggesting that the generation of mental images in different modalities is likely to be subserved by different structures of the hemisphere dominant for language. Our thorough investigation of imagery processes in all sensory modalities, as well as in the motor domain, has indeed allowed the demonstration of a modality-specific character

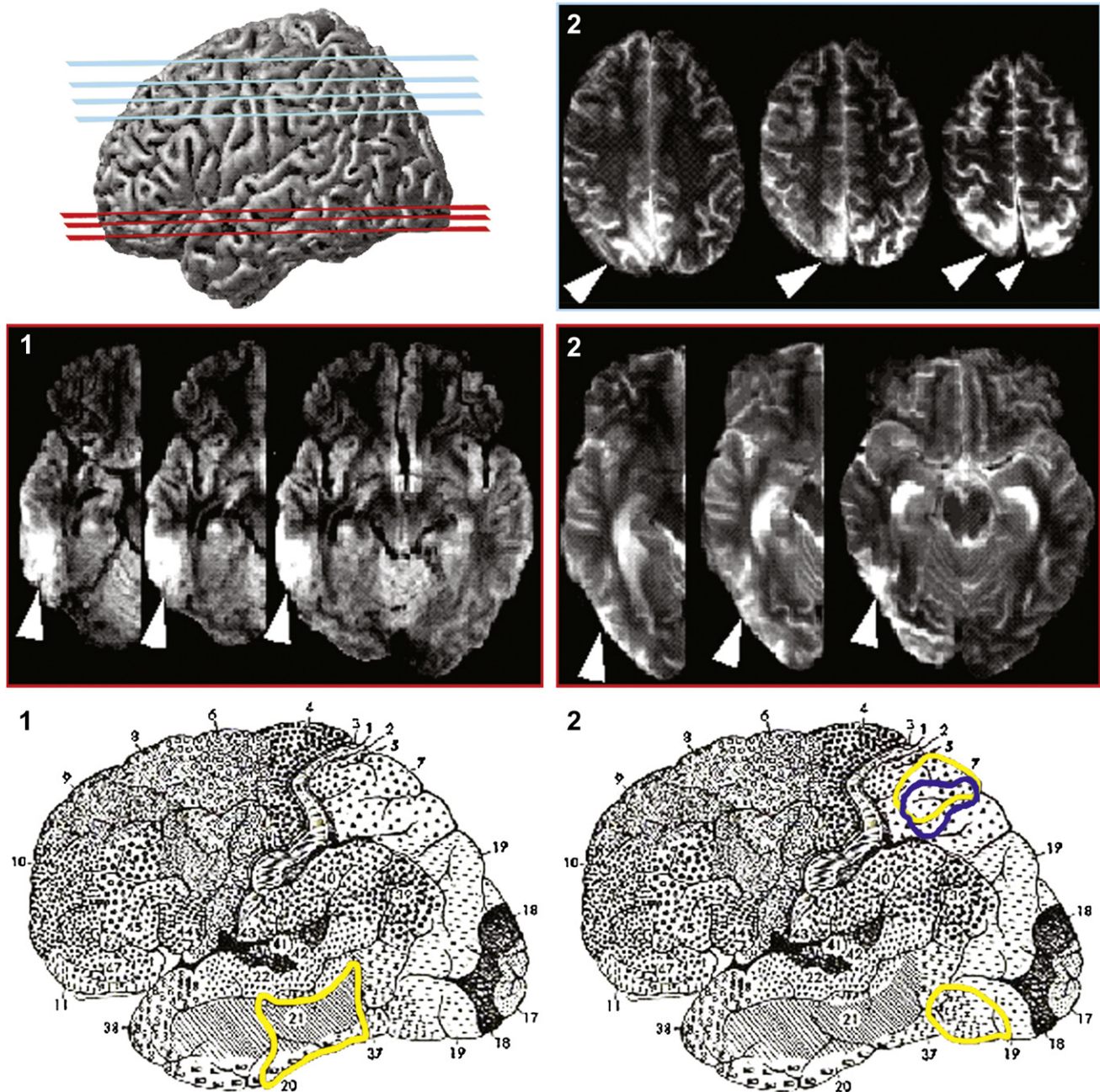


Fig. 3 – Cortical rendering (left upper panel) and selected axial views of the brain damage (white arrows) in Patient 1 (middle left panel) and in Patient 2 (upper and middle right panels). Drawings of the lesions on a standard Brodmann diagram of the brain are reported in the left (Patient 1) and right (Patient 2) lower panels. In the Brodmann maps, yellow lines outline damage to the left hemisphere and the blue line outline damage to the right hemisphere.

of mental imagery disorders following localized brain damage. Such modality specificity is proved by the fact that both patients had no difficulties with tests that assess auditory, gustatory and olfactory imagery without requiring the formation of visual images. The normal performance on the latter tests, as contrasted with the poor performance on visual imagery tests, is unlikely to depend on a comparatively greater difficulty of the latter tests, since, for example, a memory comparison of the sounds of different musical instruments, on which the

patients had no difficulty, seems hardly easier than a memory evaluation of whether an alligator's legs are short or long compared to the animal's body, which the patients conspicuously failed. A further argument against a possible role of task difficulty in determining the performance differences between visual and non-visual imagery tests is offered by Patient 2's performance on tests of vision-independent tactile imagery. Whereas Patient 1's performance on these tests was normal, that of Patient 2 was clearly not, in spite of the relative integrity

of his tactile perception. This means that the difficulty of the present non-visual imagery test was adequate to reveal the existence of performance deficits. In the case of Patient 2, such deficits can be ascribed to the presence of bilateral lesions of high-order parietal areas that are known to be involved in tactile processing and cross-modal visuo-tactile integration (Bueti et al., 2004; Driver and Vuilleumier, 2001), as well as in the mental imagery of tactile qualities of an object, such as roughness, hardness and temperature (Newman et al., 2005). As a parallel with the association of the present visual imagery disorders with the integrity of V1, it is of interest that Patient 2's primary somatosensory cortex appeared intact on both sides.

In general, the present findings support the view that modality-specific mental imagery disorders are caused by lesions of high-order cortical areas within the respective specific systems, even when the primary receiving areas within those systems are spared. This has proven true of the visual (Bartolomeo, 2002), auditory (Zatorre and Halpern, 1993) and motor domains (Johnson et al., 2002). The proposed involvement of V1 as a visual buffer shared by perception and imagery is subject to much controversy. In principle, the anatomically demonstrated back-projections from higher cortical areas may both generate an orderly activity in V1 during imagery, and shape the activity of this cortex during perception. Yet the precise modes of action of these putative top-down modulations of V1 are largely unknown. A recent fMRI investigation has revealed task- and stimulus-dependent interactions between temporo-occipital, parietal and frontal regions. Perception of faces and objects is mediated by bottom-up mechanisms arising in early visual areas, whereas top-down influences from prefrontal cortex appear to be at play during imagery of the same items. Additional top-down influences from superior parietal areas appear to contribute to the generation of mental images, regardless of their content and duration (Mechelli et al., 2004). The present finding of disordered visual imagery associated with good visual perception in the presence of an intact V1 seems complementary to the finding of a richly preserved visual imagery coupled with dense cortical blindness in a patient with nearly complete bilateral destruction of V1 (Goldenberg et al., 1995).

5. Conclusions

In conclusion, the present findings contribute to different aspects of the debate on the relationships between perception and imagery. First, they confirm that visual imagery deficits can occur quite independently from visual perception deficits. Second, they strongly support the hypothesis that the left temporal lobe plays a crucial role in visual mental imagery, in agreement with previous studies (e.g., Bartolomeo, 2002). Third, they show that the occurrence of marked visual imagery deficits is compatible with the anatomical integrity of the primary visual cortex and its normal functioning, as indicated by efficient visual perception. Fourth, they offer novel evidence to suggest that different neural substrates underlie modality-specific sensory and motor imagery, parts of the parietal lobes being most likely involved in tactile imagery.

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