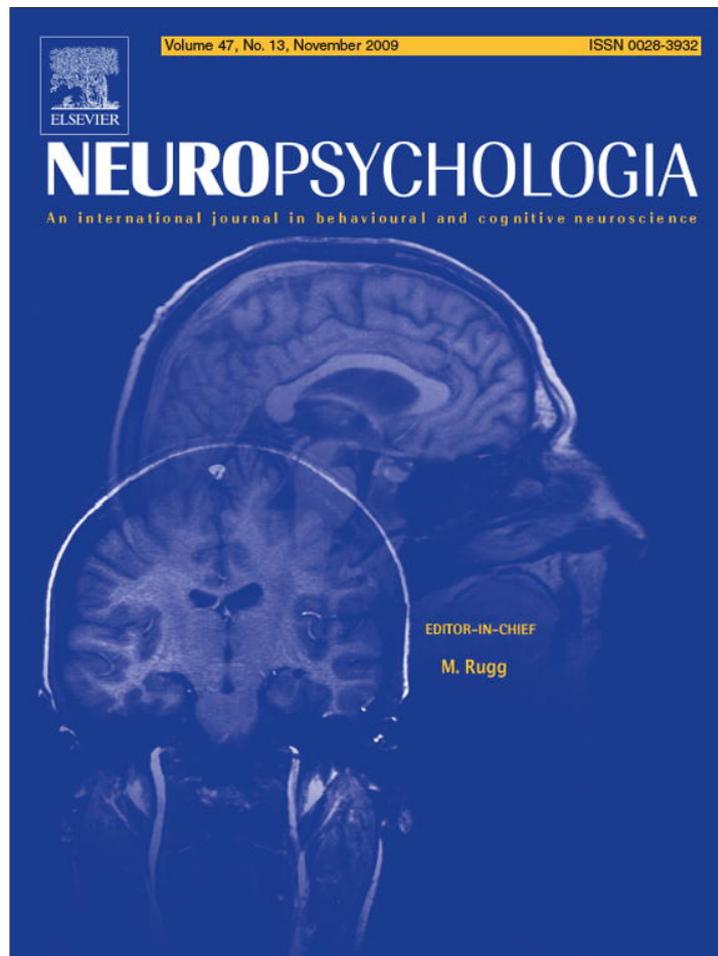


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Differential impact of posterior lesions in the left and right hemisphere on visual category learning and generalization to contrast reversal

Berthold Langguth^{a,b}, Martin Jüttner^{c,*}, Theodor Landis^d, Marianne Regard^e, Ingo Rentschler^a

^a Institute for Medical Psychology, University of Munich, Germany

^b Department of Psychiatry, Psychotherapy and Psychosomatics, University of Regensburg, Germany

^c Psychology, School of Life and Health Sciences, Aston University, Aston Triangle, Birmingham B4 7ET, UK

^d Neurology Clinic, University Hospital and Medical Faculty, Geneva, Switzerland

^e Department of Neurology, University Hospital, Zurich, Switzerland

ARTICLE INFO

Article history:

Received 15 August 2008

Received in revised form 12 June 2009

Accepted 18 June 2009

Available online 30 June 2009

Keywords:

Vision

Object recognition

Categorization

Learning

Invariance

Laterality

ABSTRACT

Hemispheric differences in the learning and generalization of pattern categories were explored in two experiments involving sixteen patients with unilateral posterior, cerebral lesions in the left (LH) or right (RH) hemisphere. In each experiment participants were first trained to criterion in a supervised learning paradigm to categorize a set of patterns that either consisted of simple geometric forms (Experiment 1) or unfamiliar grey-level images (Experiment 2). They were then tested for their ability to generalize acquired categorical knowledge to contrast-reversed versions of the learning patterns. The results showed that RH lesions impeded category learning of unfamiliar grey-level images more severely than LH lesions, whereas this relationship appeared reversed for categories defined by simple geometric forms. With regard to generalization to contrast reversal, categorization performance of LH and RH patients was unaffected in the case of simple geometric forms. However, generalization to contrast-reversed grey-level images distinctly deteriorated for patients with LH lesions relative to those with RH lesions, with the latter (but not the former) being consistently unable to identify the pattern manipulation. These findings suggest a differential use of contrast information in the representation of pattern categories in the two hemispheres. Such specialization appears in line with previous distinctions between a predominantly lefthemispheric, abstract-analytical and a righthemispheric, specific-holistic representation of object categories, and their prediction of a mandatory representation of contrast polarity in the RH. Some implications for the well-established dissociation of visual disorders for the recognition of faces and letters are discussed.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Visual object recognition critically depends on the ability to relate sensory input provided by the eyes to stored conceptual knowledge in terms of object categories (Bruner, 1957; Rosch, 1978). There is ample neuropsychological evidence to suggest that unilateral lesions in the left and right hemisphere affect perceptual categorization to a different extent. In particular the systematic studies of De Renzi, Faglioni, and Spinnler (1969) and Warrington and Taylor (1973) were among the first to demonstrate that patients with posterior right hemisphere (RH) lesions do more poorly on apperceptive tests (e.g., overlapping figures, identifying objects photographed from unusual perspectives), whereas patients with posterior left hemisphere (LH) lesions tend to have difficulty in associative tests (e.g., matching real objects to photographs of dif-

ferent items of the same class). Subsequently, this line of research culminated in various attempts of a dichotomous characterization of hemispheric differences with the common denominator of a particular right-hemispheric competence for perceptual categorization (e.g., Farah, 1990; Humphreys & Riddoch, 1984; Shallice, 1988; Warrington & Taylor, 1978).

Still, the dominance of the right hemisphere for perceptual analysis is likely to be relative rather than absolute. Patients with lesions within the right-hemisphere's visual system often can easily read and name real objects without difficulty, and also identify photographs and line drawings of objects provided they are not artificially degraded. Moreover, the visual analyses performed by the left and right hemisphere may specialize on different aspects of a given stimulus. Campbell, Landis, and Regard (1986) demonstrated this possibility with two stroke patients with a right posterior and a left posterior lesion, respectively. The two patients showed complementary performance patterns for the categorization of handwritten material and facial expressions. With handwritten material, the patient with the left posterior stroke could only analyse the text as to 'who' had written it but not what the text actually

* Corresponding author.

E-mail address: m.juttner@aston.ac.uk (M. Jüttner).

meant, whereas the situation was reversed for the patient with the right posterior stroke. Similarly, when analysing facial photographs the patient with the left hemisphere lesion could only classify face expressions referring to different emotions across different persons but could not classify face expressions corresponding to the enunciation of vowel sounds. The reverse performance pattern applied to the patient with the right hemisphere lesion. These double dissociations of performance within the same stimulus material (text and faces) imply specific differences in visual processing of the two hemispheres but a generic ability in both to make perceptual categorizations.

The role of the two cerebral hemispheres in pattern categorization has also been investigated in healthy observers. Using a divided-field paradigm Marsolek, Kosslyn, and Squire (1992) and Marsolek, Squire, Kosslyn, and Lulenski (1994) found greater priming for unchanged typographic case when words were presented initially to the right hemisphere than to the left hemisphere. In contrast, changing a letter's case (e.g., from upper case to lower case) resulted in equivalent levels of priming in both hemispheres, a result that is consistent with the idea that the right hemisphere encodes specific-exemplars better than the left one. In another study assessing repetition priming of line drawings of common objects (Marsolek, 1999) the picture of one exemplar (e.g., a grand piano) primed the picture of another exemplar of the same class (e.g., a standard piano) more effectively in the LH than in the RH. In contrast, repetition of the same exemplar (e.g., repeating the picture of the same grand piano) had larger priming effects in the RH than in the LH.

In order to explain these findings Marsolek suggested a model (Marsolek, 1995, 1999; for a different but related account see Laeng, Zarrinpar, & Kosslyn, 2003) according to which visual forms are stored in the RH within a so-called specific-exemplar subsystem, whereas such forms are stored in the LH within a so-called abstract-category subsystem. An important feature of this model is that it postulates differences of visual processing in the two subsystems (rather than confining such differences to the post-visual representation of object knowledge). More specifically, abstract-category recognition should rely on an assessment of independent features or dimensions, which may involve explicit rules and thus allow an efficient representation of information that is common to input patterns that are categorized together. In contrast, specific-exemplar recognition should follow a more whole-based processing strategy, where features are represented in combination rather than independently. Such a strategy should facilitate the discrimination of exemplars both within the same category and across different categories, thus subserving a functional role complementary to that of the abstract-category subsystem.

There have been relatively few attempts to explore the specific implications of this model for the acquisition of categories of unfamiliar visual stimuli. Marsolek (1995) trained normal participants to categorize nonsense patterns composed of line segments employing a modified version of the classical paradigm of Posner and Keele (1968). Subjects were subsequently tested in each hemi-field for their recognition of the previously learned patterns as well as for the previously unseen prototypes (i.e., the central tendencies of each category) and entirely novel distortions thereof. Participants recognized the prototype patterns more efficiently when presented to the left hemisphere (i.e., in the right visual field) than when presented to the right hemisphere (i.e., in the left visual field). No performance differences were found between the two presentation conditions for recognition of the previously seen patterns and unseen prototype distortions. These results provide support for the notion of an abstract-category subsystem based in the left hemisphere that stores information that remains relatively invariant across the specific instances of patterns belonging to the same category. Even so, the paradigm assesses hemispheric differences in

pattern category learning only indirectly, by assessing recognition performance after learning already had taken place and by testing generalization only with regard to spatial transformations.

Lesion studies also provide some evidence for a dissociation between abstract-category representation and memory for specific instances. Scheidler et al. (1992) report the case of a patient (M) with extensive occipito-temporal infarctions bilaterally in the territory of both posterior cerebral arteries. M was able to learn to classify checkerboard patterns almost as quickly and accurately as normal age-matched controls. This demonstrated that elementary visual functions such as coarse spatial resolution and discrimination of simple geometric forms were relatively unimpaired, that he was able to make decisions as to which category a given stimulus belonged and that he could synthesize a simple Gestalt out of individual elements. However, M had severe difficulty in learning a similar categorization task with compound Gabor patterns, in contrast to age-matched controls. Furthermore, M was unable to generalize the acquired class knowledge to grey-level transformed versions of the original patterns, again in stark contrast to normal observers. Thus it appears that M failed to form abstract representations of the pattern categories to accommodate generalization.

Squire and Knowlton (1995) studied an amnesic patient (EP) with extensive bilateral damage in the region of the medial temporal lobe and virtually no capacity for explicit memory. Whereas EP was unable to memorize individual exemplars in a category learning task involving dot patterns (cf. Posner & Keele, 1968) his performance at classifying novel stimuli according to whether they did or did not belong to the class training stimuli was normal. EP would recognize a prototype (unseen during learning) as a member of a category suggesting some form of abstract-category knowledge. This contrasts with some of the learning problems of patient M in the aforementioned study of Scheidler et al. (1992), which were strongly suggestive of a putative deficit within his abstract-category subsystem. However, the different location of the lesions in the two cases, their extensive bilateral extension and the complex pattern of associated disorders do not permit a straight allocation of the observed deficits in pattern category learning to the left or right hemisphere or to evaluate hemispheric differences in visual processing during such learning tasks.

The present study aimed to explore hemispheric differences in the learning and generalization of pattern categories more systematically by focussing specifically on patients with unilateral posterior, cerebral lesions in the left or right hemisphere. Such lesions often involve cortical blindness in circumscribed regions of the contralateral visual field and permit to assess the contribution of the remaining intact hemisphere in relative isolation. Seven patients with LH lesion and associated visual field defects in the right visual field, and nine with RH lesion and associated blindness in the right visual field participated. Each patient took part in two category learning experiments involving the categorization of simple geometric forms and unfamiliar grey-level images (truncated compound Gabor patterns). As posterior lesions often are accompanied by alexia (in case of LH lesions) and prosopagnosia (in case of RH lesions) our choice of stimuli avoided letter- and face-like stimuli to ensure that the categorization task could be learnt by the intact (left or right) hemisphere.

We probed the internal representations acquired in the two hemispheres by assessing generalization performance with regard to contrast-reversed versions of the learning patterns (see Jüttner, Langguth, & Rentschler, 2004). Following Marsolek's distinction, abstract-category recognition – primarily mediated by the left hemisphere – should rely on the analytical assessment of independent feature dimensions that are crucial for the discrimination of pattern categories while ignoring features without diagnostic value. Internal representations of pattern categories should therefore be invariant to contrast reversal if – as the case in our two

classification tasks – contrast polarity is not a critical attribute for category definition. On the other hand, a whole-based processing strategy, implied by specific-exemplar recognition and primarily mediated by the right hemisphere, should be more likely to result in category representations that include contrast polarity regardless of its diagnostic value. Contrast reversal should therefore impede pattern recognition based on such representations more severely.

Thus, while successful pattern categorization may be achieved by both processing mechanisms – though perhaps with varying efficiency depending on stimulus type – the differences between the mechanisms should also become manifest in a different potential to generalize to a change in contrast polarity. For RH-lesioned patients we predicted a high (possibly perfect) generalization to contrast-reversed patterns regardless of pattern type, mediated by LH-based, abstract-category representations. For LH-lesioned patients we expected generalization to rely on judging the overall-shape similarity between contrast-reversed and original versions using a RH-based, whole-based processing strategy. This would predict that performance distinctly depends on pattern type, being high in case of simple geometric forms (where a shape-based correspondence between original and contrast-reversed version is easy to establish) while significantly deteriorating in case of the visually more complex Gabor stimuli.

2. Method

2.1. Subjects

Sixteen patients with unilateral posterior lesions in the left (seven patients) or right (nine patients) hemisphere and associated visual impairments and visual field deficits participated in the study. Ten patients were in- or out-patients of the Neurological University Hospital in Geneva, Switzerland; the remaining six patients were in- or out-patients of the Neurological University Hospital in Zurich, Switzerland. Informed consent from all patients was obtained and the study was conducted according to the ethical standards laid down in the Declaration of Helsinki II.

Table 1 summarises the relevant demographic and clinical details of each patient. The difference between the median age of LH patients (59.1 years; range: 20–80 years) and RH patients (65.0 years; range: 22–78 years) was nonsignificant (Mann–Whitney test, $z = -0.74$, $p = 0.45$). Brain lesions were localised on the basis of CT and MRI scans. Visual disorders were established by neuropsychological assessment. Visual field deficits were validated by automated, static perimetry. Furthermore, for all patients visual acuity was determined as part of their neuro-ophthalmologic assessment and yielded values of 0.5 or better in at least one eye.

2.2. Apparatus

Stimuli were presented on a 17-in. monitor (Lucius & Baer GBM 2310; spatial resolution of 1024 × 768 pixel screen resolution, 72 Hz refresh rate) that was controlled by a personal computer. The background luminance L_0 of the screen was kept constant at 70 cd/m².

The nominal viewing distance for all stimuli was 100 cm. However, as some of the participants had impaired visual acuity they were encouraged to choose a viewing distance that was optimal for them. Because the participants were suffering from visual field defects they were also given the possibility to freely choose a fixation point such that the patterns could be completely perceived within their intact hemifield.

2.3. Stimuli

Each of the two experiments involved a set of 15 grey-level patterns, divided into three classes with five patterns per class. In Experiment 1 the set consisted of five squares (class 1), five triangles (class 2) and five circles (class 3) of varying size. At the nominal viewing distance of 100 cm the side length (diameter) of the patterns varied between approximately 0.53° and 1.06° (mean: 0.8°) of visual angle. For the learning phase of the experiment, the patterns were shown with a Weber contrast relative to the background that was kept at –0.61. Thus, the patterns appeared dark against the background (Fig. 1A). For the generalization phase in Experiment 1, a second version of the stimuli was generated by reversing contrast polarity as illustrated in Fig. 2.

Experiment 2 employed a set of unfamiliar grey-level images based on compound Gabor gratings. Such gratings result from the superposition of two sine-wave gratings, a fundamental plus its third harmonic, within a Gaussian aperture and have a well-defined one-dimensional part structure in terms of bright and dark bars along their horizontal symmetry axis. In the past, compound Gabor gratings have been used in numerous categorization studies (e.g., Jüttner & Rentschler, 1996; Jüttner & Rentschler, 2000; Kahana & Bennett, 1994; Notman, Sowden, & Özgen, 2005), as they stimulate learning due to their high unfamiliarity while minimizing effects of prior knowledge. The present experiment re-used a set of 15 Gabor stimuli from a previous study on category learning (set I in Jüttner et al., 2004). Within the Fourier feature space used to specify the patterns, the stimuli formed three clusters of five samples each (see Jüttner et al., 2004 for details), each defining one category to be learned by the participant. To facilitate the categorization of these patterns by patients, the Gabor stimuli were post-processed by removing all image parts with intermediate grey-level values. Image pixels with luminance values in the interval $[L_0 - (a + b)/2, L_0 + (a + b)/2]$ were set to the level of L_0 , where L_0 denotes the mean luminance of the background and a and b are the amplitudes of the fundamental and third harmonic of the Gabor gratings, respectively. This manipulation produced more accentuated versions of the patterns and has been shown to greatly facilitate category learning in normal subjects (Jüttner et al., 2004). The resulting set of patterns is shown in Fig. 1B. The patterns had a Michelson contrast of 0.71 and subtended 0.8 deg of visual angle at the nominal viewing distance of 100 cm. For the generalization phase in Experiment 2, a second version of contrast-reversed patterns was generated as illustrated in Fig. 2.

2.4. Procedure

Experiments 1 and 2 employed the same procedure and only differed in regard to the stimuli used. Each experiment was divided into two parts, learning and generalization test. The first part used a supervised learning schedule (see Jüttner & Rentschler, 1996; Rentschler, Jüttner, & Caelli, 1994) and consisted of a variable number of learning units. Each learning unit had two phases, training and recognition test. During the training phase, each pattern was shown three times in random order for 200 ms, followed by a number specifying the class (1, 2, 3) to which the pattern belonged. The class label was displayed for 1000 ms, with an interstimulus interval of 500 ms relative to the offset of the learning pattern. During the test phase of each learning unit, which served to monitor the learning status of the subject, the patterns were shown once in random order for 200 ms and classified by the subject by

Table 1
Demographic and clinical details of participating patients.

Patient/sex	Age	Lesion	Localisation of lesion	Duration of lesion	Visual field defect	Agnosias
AD/m	31	Infarct	Right temporo-occipital	2a	HA, left	None
AG/m	66	Infarct	Left temporo-occipital	16m	HA, right	Alexia, colour agnosia
EM/w	57	Operation for glioma	Right temporo-parieto-occipital	21a	HA, left	None
GW/w	28	Thrombosis	Left temporal	7d	HA, right	Alexia
HH/m	65	Infarct	Right parietal to orbito-frontal	1m	NL, left	None
JC/w	79	Infarct	Right temporal superior and right parietal	3m	NL, left	Anosognosia
KD/w	67	Infarct	Right temporo-occipital	12a	HA, left	Prosop- and topograph agnosia
MA/w	80	Infarct	Left temporo-parieto-occipital	10d	HA, right	None
PB/m	46	Operation of an arteriovenous malformation	Left occipital	2a	HA, right	None
RC/m	64	Operation for glioma	Right temporal	2m	HA, left	None
RG/m	79	Infarct	Left occipital	2m	HA, right	None
RR/m	82	Hemorrhage	right occipital	14d	QA, left superior	None
SB/m	64	Infarct	Right occipital	1m	QA, left superior	None
VG/w	52	Hemorrhage	left temporo-occipital	14d	HA, right	None
WM/m	76	Infarct	Bilat. occipito-temporal, right frontal	7a	HA, bilateral superior	Prosopagnosia, pure alexia
ZL/w	59	Infarct	Left occipital	7d	HA, right	None

Note: m/f: male/female; duration of lesion: time between onset of brain lesion and testing given in years (a), months (m) or days (d); visual field defect: HA: hemianopia, QA: quadrantanopia, NL: hemineglect.

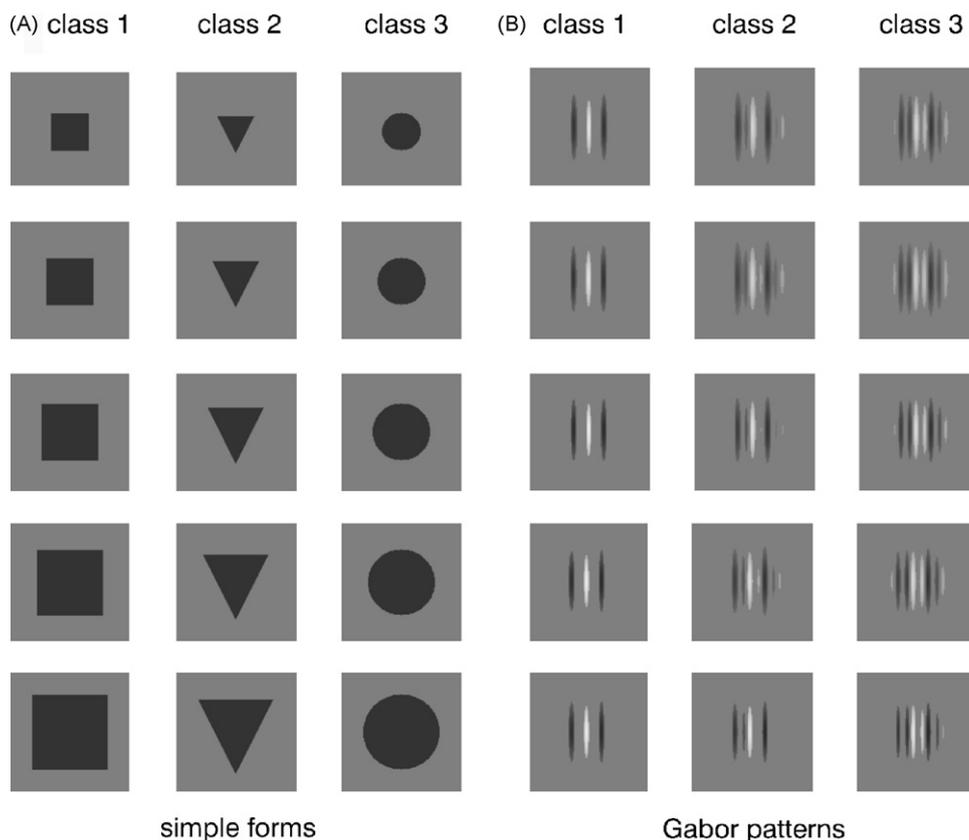


Fig. 1. Two sets of patterns used for category learning. (A) In Experiment 1 the set consisted of 15 simple geometric forms (five squares, five triangles, five circles) of varying size. Each form defined one pattern class to be learnt by the participant. (B) Experiment 2 employed a set of 15 unfamiliar grey-level images, divided into three classes of five samples each. The stimuli were based on a set of compound Gabor gratings used in a previous study (set 1 in Jüttner et al., 2004). To facilitate the categorization of these patterns by patients, accentuated versions of the Gabor gratings were generated in which all image parts with intermediate grey-level values had been removed.

pressing the appropriate button on the computer keyboard. Normally, the series of learning units continued until the observer had achieved the learning criterion of error-free classification (100% correct) in one recognition test. However, the learning procedure was also terminated if classification performance showed no further increase in consecutive learning units and if the patient reported that he/she was unable to improve their performance any further.

Once the subjects had completed learning they entered the second part of the experiment, the generalization test. Here their ability was assessed to recognize contrast-inverted versions of the previously learned patterns. Each test pattern was presented and classified three times in random order, leading to 45 categorization trials per subject. The timing parameters were the same as in the recognition tests during the preceding supervised learning. Upon completion of the generalization test in Experiment 2 participants were asked whether they had noticed any difference between the pictures used in the first part and those in the second part of the experiment, and if so how this difference could be described.

All trials requiring a response on part of the patient, i.e. the recognition test trials during the supervised learning and the generalization test trials, were self-

paced to allow additional breaks where needed. It was intended that participants carried out both experiments with a short break in between. Experiment 1 always had to be completed before starting with Experiment 2. As Experiment 1 involved a relatively easy task, the categorization of simple geometric forms, this ensured that patients were already familiar with the procedure when they approached the more demanding task of learning to categorize unfamiliar patterns in Experiment 2. Furthermore, this procedure allowed the use of Experiment 1 as a test to ensure that patients were capable to complete a category learning task of the given structure (i.e., involving three classes and five patterns per class). Patients normally completed the two experiments including breaks within a single 1–2 h session.

2.5. Data analysis

The data was analysed in terms of the proportion of correct responses extracted from the classification matrix of each observer. Owing to the relatively small sample size, all pairwise group comparisons were based on nonparametric randomization tests of the scores using NPFact version 1.0 (May, Hunter, & Gabriel, 1993) and considering all possible permutations. The same software package was used to consolidate standard Analysis of Variance measures in factorial designs. Here the randomization tests involved 100,000 permutations of each data set.

3. Results

As already mentioned, a major purpose of Experiment 1 was to familiarize the patients with the task and to ensure that they were in principle able to learn pattern categories. Furthermore, any emerging group difference was expected to favour patients with RH lesion—in line with previous reports of a LH advantage for familiar stimulus material (e.g., Marzi & Berlucchi, 1977). Against this baseline, Experiment 2 addressed, using sets of unfamiliar patterns, the main hypotheses of the paper concerning hemispheric differences for the representation of pattern categories and related differences in the susceptibility to changes in appearance induced by contrast reversal.

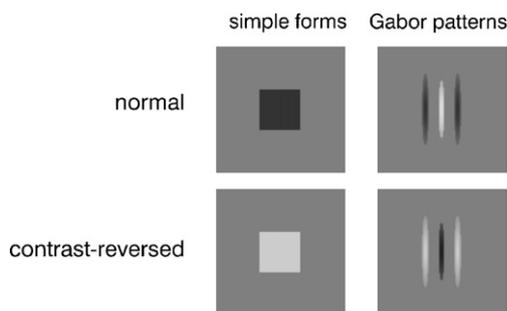


Fig. 2. Illustration of normal and contrast-reversed patterns in Experiment 1 (simple forms) and Experiment 2 (Gabor patterns). In each experiment, participants were first trained to categorize the normal versions of the patterns. The learning procedure was followed by a generalization test using the contrast-inverted versions.

Table 2A
Results of patients with LH lesions in Experiments 1 and 2.

Patient	Visual field defect	Exp. 1 (simple geometric forms)				Exp. 2 (Gabor patterns)				
		p_{L1}	N	p_{MAX}	p_{INV}	p_{L2}	N	p_{MAX}	p_{INV}	con. rev. i.d.
AG	HA, right	.33	2	1.0	1.0	.94	3	1.0	.80	+
GW	HA, right	.53	3	1.0	.89	.60	8	.94	.67	+
MA	HA, right	.33	4	.30	○	○	○	○	○	○
PB	HA, right	1.0	1	1.0	1.0	.80	5	.94	.85	–
RG	HA, right	1.0	1	1.0	1.0	.60	3	.73	.38	+
VG	HA, right	.40	4	.60	○	○	○	○	○	○
ZL	HA, right	.33	4	1.0	1.0	.86	4	1.0	.87	+

Note: Visual field defect: HA: hemianopia, QA: quadrantanopia, NL: hemineglect; p_{MAX} : peak recognition rate during supervised learning; N : number of learning units; p_{L1} , p_{L2} : exposure-equated learning performance after one (Experiment 1) resp. two (Experiment 2) learning units; p_{INV} recognition rate for contrast-reversed patterns; ○: patient decided to abandon experiment; con. rev. i.d.: correct (+) or incorrect (–) identification of pattern change during generalization test as contrast reversal.

Table 2B
Results of patients with RH lesions in Experiments 1 and 2.

Patient	Visual field defect	Exp. 1 (simple geometric forms)				Exp. 2 (Gabor patterns)				
		p_{L1}	N	p_{MAX}	p_{INV}	p_{L2}	N	p_{MAX}	p_{INV}	con. rev. i.d.
AD	HA, left	1.0	1	1.0	1.0	.90	2	1.0	.93	–
EM	HA, left	1.0	1	1.0	1.0	.50	4	.80	.73	–
HH	NL, left	1.0	1	1.0	.89	.26	12	.33	.22	–
JC	NL, left	.40	2	1.0	1.0	.40	2	.40	○	○
KD	HA, left	1.0	1	1.0	.98	.50	5	.80	.78	–
RC	HA, left	1.0	1	1.0	.89	.33	3	.27	.33	–
RR	QA, left sup.	1.0	1	1.0	.96	.53	7	.73	.57	–
SB	QA, left sup.	1.0	1	1.0	1.0	.80	4	.93	.93	+
WM	HA, sup.	1.0	1	1.0	.98	.33	13	.47	.38	–

Note: Visual field defect: HA: hemianopia, QA: quadrantanopia, NL: hemineglect; p_{MAX} : peak recognition rate during supervised learning; N : number of learning units; p_{L1} , p_{L2} : exposure-equated learning performance after one (Experiment 1) resp. two (Experiment 2) learning units; p_{INV} recognition rate for contrast-reversed patterns; ○: patient decided to abandon experiment; con. rev. i.d.: correct (+) or incorrect (–) identification of pattern change during generalization test as contrast reversal.

The data of Experiments 1 and 2 presented in the following are supplemented by the results of some further assessments that were carried out with the patients studied in Geneva.

3.1. Experiment 1

Here the participants first had to learn to classify simple geometric forms of varying size according to their shape into three categories. They were then asked to categorize contrast-reversed versions of the previously learned shapes. Tables 2A and 2B summarise the results for LH-lesioned and RH-lesioned patients, respectively. In the table p_{MAX} denotes the peak performance in the recognition tests during the supervised learning phase, N represents the number of learning units necessary to reach p_{MAX} , and p_{INV} shows the relative recognition rate for the contrast inverted test patterns. As a further index to assess learning progress we computed p_{L1} , the recognition performance after the first learning unit (note that according to Tables 2A and 2B each patient conducted at least one learning unit in Experiment 1, hence p_{L1} permits an exposure-equated comparison of performance after the same amount of learning experience).

Concerning learning, eight out of the nine patients with RH lesions were able to classify the patterns correctly after one learning unit; only patient JC required two learning units. In contrast, among the seven patients with LH lesions only two achieved a correct classification of all patterns in the first learning unit. Two of the remaining five patients reached the criterion within four learning units. All these patients had difficulty in understanding that the task was to classify patterns according to pre-defined labels. Patients ZL and GW initially assigned patterns of the same category into the same class but allocated them to the wrong class label; for example, they classified the triangles as class 1 rather than class 2. Patient MA tried to classify the patterns according to size, and patient VG classified in a non-systematic, haphazard way. Both MA and VG

decided to terminate the experiment after the fourth learning unit, and did not take part in the subsequent Experiment 2.

With MA and VG excluded from further analysis at group level, LH patients on average required 2.4 learning units to achieve an error-free classification, significantly longer ($p < 0.05$, 1-tailed) than RH patients (mean: 1.1 learning units). Furthermore, as illustrated in Fig. 3, exposure-equated learning performance p_{L1} after the first learning unit was significantly higher ($p < 0.05$, 1-tailed) in RH patients (mean: 0.93) than in LH patients (mean: 0.63). With regard to learning, both performance measures therefore indicate an advantage of the LH group

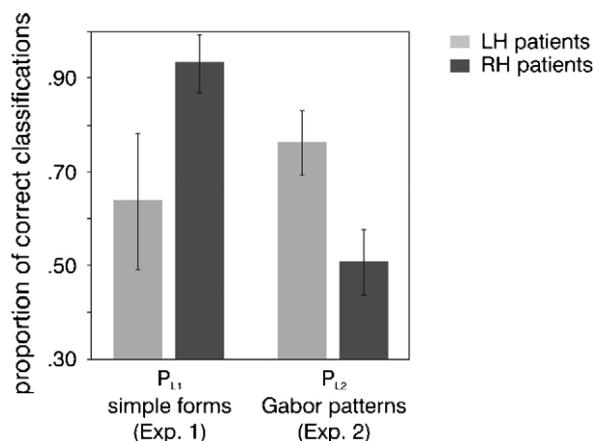


Fig. 3. Group comparison of exposure-equated learning performance in Experiments 1 and 2. The bars show for LH and RH patients the mean scores of p_{L1} (p_{L2}), the recognition performance after one (two) learning units (the minimum number of learning units each patient completed in Experiments 1 and 2, respectively). Note the complementary performance pattern displayed by LH and RH patients with regard to the categorization of simple geometric forms (Experiment 1) and Gabor stimuli (Experiment 2).

for the acquisition of categories defined by simple geometric forms.

Reversal of contrast polarity had only a very mild impact on categorization. After having reached a perfect classification in the learning stage of the experiment, mean performance during the generalization test (involving the contrast-reversed patterns) dropped to 0.98 for LH patients and to 0.96 for RH patients. There was no significant difference in performance between the two groups ($p = 0.55$).

3.2. Experiment 2

In Experiment 2 the participants first had to learn to classify unfamiliar grey-level patterns into three pre-defined categories. They were then asked to categorize contrast-reversed versions of the previously learned patterns. The results for the two parts of the experiment are again summarised in [Tables 2A and 2B](#). As each patient in Experiment 2 conducted at least two learning units we computed, in analogy to Experiment 1, p_{L2} as exposure-equated index of learning performance after these two units.

Concerning learning, all participating patients with LH lesion reached a peak classification performance of at least 0.73, significantly above chance, with a group mean of 0.92. In contrast, four out of nine patients with RH lesions (JC, WM, RC, HH) failed to reach a classification performance that was significantly above chance ($p_s > 0.19$; binomial test), with one patient (JC) terminating the experiment prematurely after the second learning unit. Among the remaining three of these patients, WM correctly classified some patterns of class 1 and systematically misclassified some patterns of class 2 (as class 1) and of class 3 (as class 2). RC reported that he could not establish a criterion that would allow him to assign the patterns into the three classes. Similarly, the data of HH showed no systematicity in the way the patterns were classified. For the five RH patients who displayed category learning above chance level the mean peak performance was 0.85.

Because some of the patients did not reach the criterion of an error-free classification in Experiment 2, LH–RH group comparisons of learning performance were based on p_{L2} scores only. For LH patients the mean exposure-equated learning performance after the second learning unit was 0.76, significantly higher ($p < 0.05$, 1-tailed) than the mean value of 0.50 observed for RH patients. Thus, LH and RH patients showed a dissociation of learning performance complementary to the one observed in Experiment 1, and with a relative advantage of LH patients for the learning of pattern categories defined by Gabor stimuli ([Fig. 3](#)).

To assess the impact of contrast reversal on categorization performance we combined, as illustrated in [Fig. 4](#) (solid bars), the data of the peak performance achieved during learning (i.e., the p_{MAX} scores) and of the performance during the generalization test (p_{INV}). A 2×2 mixed-model ANOVA was conducted with task (p_{MAX} vs. p_{INV}) as within-subjects and lesion side (left vs. right) as between-subjects factor. Levene's test of equality of error variances and Box's test of equality of covariance matrices were both nonsignificant. The ANOVA yielded a significant main effect of task ($F(1,11) = 30.89$, $p < 0.0001$) as well as a significant interaction between task and lesion side ($F(1,11) = 9.92$, $p < 0.01$). Both effects were confirmed by additional randomization tests based on 100,000 permutations of the data set yielding $p < 0.001$ and $p < 0.05$, respectively. The significant interaction term demonstrates that LH and RH patients were differently affected by contrast inversion in Experiment 2, with a relative advantage of RH patients for generalizing categorical knowledge across this particular change in pattern appearance. This advantage did not depend on the floor effects introduced by the data of the three RH patients who, as mentioned earlier, had failed to reach a classification performance above chance during learning. Repeating the ANOVA without the data of these patients (cf.

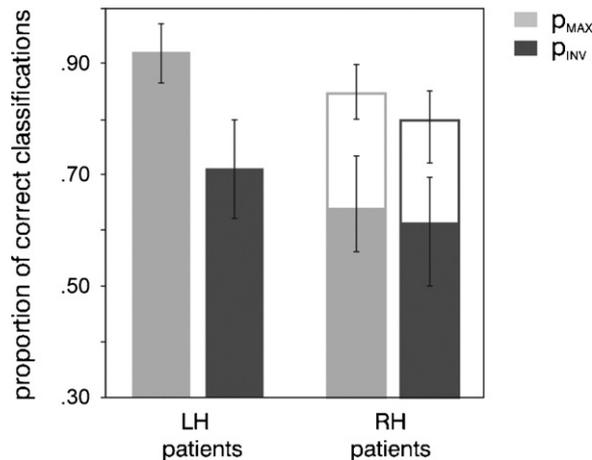


Fig. 4. Impact of contrast inversion on the classification of the Gabor patterns in Experiment 2. The bars show for LH and RH patients the mean scores of the peak performance achieved during learning (p_{MAX}) and of the correct classifications of the contrast-reversed patterns in the generalization test (p_{INV}). Note the reduced impact of contrast reversal on classification performance of RH patients, regardless whether the data is pooled across all RH patients (solid bars) or across only those with a p_{MAX} score above chance level (open bars).

[Fig. 4](#), open bars) replicated the main effect of task ($F(1,8) = 24.91$, $p < 0.001$) and, crucially, the interaction of task and lesion side ($F(1,8) = 6.98$, $p < 0.05$). Again, both effects were consolidated by additional randomization tests ($p < 0.001$ and $p < 0.05$, respectively).

The group differences with regard to generalization to contrast reversal are also reflected in differences in the ability to detect the change in contrast polarity (cf. last column in [Tables 2A and 2B](#)). While a majority of patients with LH lesions correctly identified the change in the patterns between learning and generalization as one of contrast reversal only one out of eight RH-lesioned patients who completed Experiment 2 was able to detect this change, yielding a significant difference at group level ($p < 0.05$, Fisher's exact test).

Remarkably, the only RH patient who correctly identified the pattern change suffered from anopia confined to one quadrant of the visual field. None of the RH-lesioned patients with hemianopia or hemineglect was able to do this identification. Rather they characterized the pattern modification as a change in slimness (HH) or height (WM, EM) of the bars within the patterns, or more generally as a change in pattern composition (AD) or clarity (KD).

3.3. Further assessments

Nine patients (three with LH lesion, six with RH lesion) studied in Geneva completed two additional tests to assess their ability to discriminate between normal black and white photographs (positives) and their contrast-reversed versions (negatives). There were 18 photographs (picture size: 9 cm \times 13 cm), 6 of them showing everyday objects (e.g., pushchair, padlock, kettle) while the remaining 12 were portraits of unknown persons. For each of these photographs the corresponding negative was produced.

In the first test the participant was shown in random order the positive and the corresponding negative of each of the 18 pictures. The task was to decide for each picture pair which image was the more realistic representation. The number of correct discriminations was scored.

Six of the nine patients chose the correct picture (i.e., the positive) in all 18 picture pairs. Two patients with RH lesions (JC and RC) had difficulty in solving the task for certain picture pairs: JC selected the negative as the more realistic representation in 4 out of the 6 pairs of object pictures, and in 3 out of 12 pairs of portraits; RC selected the negative in 7 out of the 12 pairs of portraits;

he correctly solved the task for all picture pairs of objects but was unable to detect the change of contrast polarity. Patient PB was unable to tell any difference between the positive and the negative of the image pairs. Both versions appeared to him as equally realistic representations.

The second test only involved the photographs of the portraits and their negatives. Subjects were given one positive photograph at a time in random order. For each positive they had to choose the corresponding negative. The number of correct assignments and the total time needed to complete this task for all 12 portraits were measured.

Eight out of nine patients assigned the correct negative to each of the 12 positives. Patient RC succeeded in this task with only 7 of the 12 portraits. The total time needed to complete the task varied across patients between 1 min 20 s and 6 min. There was no significant correlation between the speed in this perceptual matching task and generalization performance in Experiment 2 (Spearman's $\rho = -0.46$, $p = 0.35$).

4. Discussion

In two experiments involving different sets of stimuli we have demonstrated that unilateral posterior lesions in either the left or right hemisphere may have a differential impact on the acquisition and generalization of pattern categories. Lesions in the right hemisphere impeded the learning of unfamiliar grey-level images more severely than lesions in the left hemisphere, whereas this relationship appeared reversed for the learning of categories defined by simple geometric forms. This double dissociation rules out explanations in terms of deficits in early visual processing, decision making or other unspecific effects of the brain lesions.

Furthermore, no asymmetries have been found for most elementary visual performance (like acuity) measures (e.g., Zihl & Cramon, 1985). With regard to contrast sensitivity as a function of spatial frequency the evidence is mixed but may be attributed to task differences (cf. Rao, Rourke, & Whitman, 1981; Silva et al., 2008; but: Beaton & Blakemore, 1981; Kitterle & Kaye, 1985; Peterzell, Harvey, & Hardyck, 1989). However, this should not have affected our results as all our patterns were high-contrast stimuli, i.e. far above threshold. Moreover, it has been proposed that LH–RH sensitivity differences may actually reflect hemispheric criterion changes (Peterzell et al., 1989), to which forced-choice procedures such as the classification tasks in our experiments are unsusceptible.

With regard to generalization to contrast reversal, categorization performance of LH and RH patients was virtually unaffected in case of simple geometric forms. However, categorization of contrast-reversed grey-level images distinctly deteriorated for patients with LH lesions relative to those with RH lesions. Again, these differences could not be attributed to visual processing of contrast information per se. Additional assessments involving the discrimination between and matching of contrast-reversed pictures revealed no systematic differences between the two subgroups of tested patients.

These LH–RH differences emerged despite the inevitable variation that existed within each patient group with regard to aetiology, location and extent of the lesion as well as associated visual deficits. Typically, these intra-group variations worked against differences at group level: for example, PB (within the LH-lesioned group) produced an exceptional pattern of results as in none of the assessments was he able to distinguish between an image and its contrast-reversed version. With regard to learning his performance also appeared more in line with that of other RH rather than LH patients. As for a possible explanation, one could speculate that the congenital nature of PB's arteriovenous malformation may have affected his development of hemispheric

complementarity with the intact right hemisphere taking over part of the role of the left hemisphere in information processing, thus causing this particular pattern in the behavioural data. Conversely, SB was the only patient within the RH-lesioned group who could identify the pattern manipulation during the generalization test as a reversal of contrast. However, his visual field defect was restricted to one quadrant only. None of the other RH patients with hemianopia or hemineglect was able to do this identification, whereas the majority of LH patients were successful in this task. The cases of PB and SB demonstrate that the variability among patients had an attenuating effect on the group differences, rendering our LH–RH group comparison particularly conservative.

Our results therefore imply a differential processing of visual stimuli during category learning in the left and right hemisphere. Consideration of the nature of the stimuli in the two experiments suggests a number of explanations for the emerging differences between RH and LH patients. In the following, we will consider each of these explanations in more detail.

One distinguishing feature between the stimuli used in Experiments 1 and 2 is their different degrees of familiarity and ease with which they could be verbalized. Patterns in Experiment 1 were familiar geometric forms with common labels (“triangle”, “square”, “circle”) that had to be mapped onto the pre-defined labels (“1”, “2”, “3”) of the categories in the learning task. In contrast, the patterns in Experiment 2 were highly unfamiliar and could not readily be related to any pre-existing concepts. Rather, the participants had to learn to relate these spatial patterns to the pre-defined categories and their labels during the supervised learning procedure. The observed advantage of the RH-lesioned group (i.e., patients with intact LH) in Experiment 1 therefore conforms to the well-documented superiority of the left hemisphere for the processing of familiar stimulus material (e.g., Marzi & Berlucchi, 1977), whereas the relative advantage of the LH-lesioned group (i.e., patients with intact RH) in Experiment 2 appears compatible with previous work postulating a competence of the right hemisphere for the analysis of novel stimuli (e.g., Goldberg & Costa, 1981; Laeng & Rouw, 2001; Marzi & Berlucchi, 1977; Marzi, Tassinari, Tressoldi, Barry, & Grabowska, 1985). A potential problem for this explanation is the difference between the two groups with regard to generalization to contrast reversal. Whereas LH-lesioned and RH-lesioned patients were both virtually unaffected by a change of contrast polarity in case of the simple geometric forms in Experiment 1, the same manipulation of pattern appearance in Experiment 2 clearly had a more detrimental effect on recognition performance for LH-lesioned relative to RH-lesioned patients, with the latter (but not the former) being even unable to identify the pattern manipulation as one of contrast reversal. This indicates that the differences between the two groups are better characterized in terms of a hemispheric specialization for the processing of certain visual attributes (even for the same stimulus material) rather than in terms of a specialization for the processing of certain stimulus types, like familiar vs. unfamiliar patterns.

A hemispheric specialization for different types of visual attributes has been proposed by Hellige and Michimata (1989), Kosslyn et al. (1989) and Rybash and Hoyer (1992) (see Jager & Postma, 2003, for a review). Accordingly, the right hemisphere possesses greater competence for the evaluation of metric coordinate representations, whereas the left hemisphere shows an advantage for the processing of categorical spatial relations. Coordinate relations specify precise spatial locations of objects or object parts in terms of metric units and give exact distances. For the classification of Gabor patterns in Experiment 2 it is necessary to establish the spatial relationships between the parts of these patterns, i.e. the bright and dark bars. Computer simulations in the context of previous work involving similar stimulus material (Jüttner et al., 2004; Rentschler & Jüttner, 2007) suggest that this requires con-

sideration of both part-specific (e.g., position) and part-relational (e.g., distance) attributes, i.e. the type of metric spatial relationship for which an advantage of the RH is to be expected. In contrast, categorical spatial relations refer to discrete-valued relationships that result from assigning spatial configurations or a range of positions into an equivalence class without defining exact metric properties. This type of attribute seems adequate to distinguish pattern classes defined by simple geometric forms which differ in terms of simple contour properties like the number and basic arrangement of vertices. However, while the notion of a RH specialization for metric processing and a LH specialization for categorical attributes appears compatible with our learning data it remains tacit as to the effect of contrast reversal, i.e. a change in appearance that leaves the spatial relationships unaltered. It therefore offers no account for the left–right differences emerging in the generalization test.

A third account, that in a way combines the elements of the ideas of stimulus specialization and attribute specialization, is the notion of dissociable neural subsystems operating in parallel in the two hemispheres and encoding different aspects of the learning stimuli (Marsolek, 1995, 1999). As outlined earlier, according to this account the right hemisphere processes specific instances (or examples) of a category, whereas the left hemisphere encodes a more abstract-category representation. Importantly, this theory predicts a different processing of pattern attributes within the two subsystems. Abstract-category recognition should rely on an analytical assessment of independent features or dimensions and involve explicit attribute rules. By contrast, specific-exemplar recognition should be based on a more whole-based processing strategy, where features are represented in combination rather than independently.

On this basis, the classification task in Experiment 1 requiring the independent assessment of the dimensions shape and size would be relatively straightforward to be accomplished by the abstract-category subsystem dominant in the left hemisphere. The classification of the more complex stimuli in Experiment 2 albeit possible would appear considerably more difficult for this subsystem, because the larger number of pattern components (i.e., the bright and dark bars) and the extensive reservoir of potential attributes (e.g., part positions, relative distances, relative size) describing part relations make it more difficult to establish abstract rules for category membership. Conversely, it should be more difficult for the exemplar-specific subsystem dominating in the right hemisphere to separate the pattern dimensions shape and size in Experiment 1, whereas learning in Experiment 2 should be facilitated because the whole-based representation of the patterns as category-specific exemplars would make their analytical decomposition into parts and attributes obsolete.

A differential processing of visual attributes in the left and right hemisphere would also account for differences in generalization to contrast reversal, if one assumes that the whole-based representation of exemplars in the right hemisphere includes information on contrast polarity as a mandatory component. The change in appearance induced by contrast reversal would then make a matching to stored exemplars distinctly difficult, unless (as in Experiment 1) global shape can be used to establish the correct correspondence between original and contrast-reversed version. Conversely, a left-hemispheric abstract representation of categories in terms of analytic rules of pattern parts and part-relational attributes could in principle omit relative contrast if other attributes (such as size, distance, aspect ratio) are sufficiently diagnostic for the individual categories. In this case the resulting category representation should be invariant to contrast reversal.

A rule-based category representation in the left hemisphere appears compatible with reports of an increased left frontal activation in analytic problem solving (Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997), working memory tasks with verbal and

analytic elements (Smith & Jonides, 1997) and the participation of left hemisphere areas in formal, content-independent reasoning (Wharton & Grafman, 1998). In an fMRI study Seger et al. (2000) reported a left dorsolateral frontal activity in a task of visual category learning in participants that showed high levels of classification performance, and discussed the possibility that such activation could reflect verbal rule formation during the induction of pattern category knowledge. For normal subjects and a non-lateralized stimulus presentation we have shown in computer simulations of behavioural data (Jüttner et al., 2004) that category learning of compound Gabor gratings (i.e., stimuli similar to those used in the present study) relies on production rules that combine multiple attributes representing either properties of individual pattern parts or those of part relations. Moreover, these simulations found the relative proportion of contrast-invariant attributes to predict how well class concepts relying on these attributes could be generalized to contrast inversion. Taken together, this evidence suggests that RH patients in the present study accomplish the learning task by forming abstract, rule-based category representations that primarily reside in the intact left hemispheres, make little use of contrast information and, as a direct consequence, are largely invariant to a reversal of contrast polarity. Such type of representation could be regarded as a conceptual extension of previously hypothesized LH-based networks for canonical object representations with their invariance towards mirror reflections (Davidoff & Warrington, 1999, 2001).

With regard to the postulated exemplar-specific category representation in the right hemisphere the evidence is more indirect. Seger et al. (2000) report a distinct right prefrontal and inferior parietal activity during the early stages of their visual category learning task and relate this activation to the processing of specific pattern instances of each category. Such activation is consistent with previous work showing the involvement of right prefrontal and parietal areas during visual reasoning and visuo-spatial memory tasks (Jonides et al., 1993; Smith & Jonides, 1997). For exemplars of familiar categories, a right hemisphere advantage has been observed in picture name verification tasks (Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997; Laeng et al., 2003). For unfamiliar grey-level (compound Gabor) patterns we have recently shown that categories of such patterns presented in the left visual field (i.e., to the RH) are distinctly faster learned and better generalized to other locations than those learnt in the right visual field (i.e., with the LH) (Jüttner & Rentschler, 2008). These results are consistent with the advantage of LH patients during the categorization of the Gabor patterns in Experiment 2. Moreover, the better generalization of RH representations to positional changes appears complementary to the better generalization of LH representations to contrast reversal observed in the present study. Such complementarity indicates that generic perceptual invariance is mediated jointly by category representations in the two hemispheres rather than by a single, unilateral one.

Among the patients with LH lesion, two (GW, AG) showed symptoms of alexia, and among those with RH lesion two (WM, KD) displayed symptoms of prosopagnosia. The results of these patients did not substantially differ from those with lesions on the same side but without visual recognition disorders. On the one hand, this suggests that the observed differences for category learning and generalization to contrast reversal were not associated with the disorders per se but reflect properties of the residual recognition of the visual system within the intact hemisphere. On the other hand, the well-documented dissociative character of alexia and prosopagnosia (see e.g., Grüsser & Landis, 1991; Hécaen & Angelergues, 1956; Hoff & Pötzl, 1937) can be related to the differential processing of contrast information in the two hemispheres. The recognition of letters (affected in alexia) and other common objects is known to be invariant to contrast reversal (Galper, 1970;

Hayes, Morrone, & Burr, 1986; Subramaniam & Biederman, 1997), in accordance with the relative insensitivity to changes in contrast polarity in RH-lesioned individuals in the present study. The recognition of faces (affected in prosopagnosia) crucially depends on the use of contrast information and is severely disrupted by contrast reversal (Galper, 1970; Hayes et al., 1986; Liu & Chaudhuri, 1997; Nederhauser, Yue, Mangini, & Biederman, 2007), consistent with the relative sensitivity to changes in contrast polarity shown by LH-lesioned patients. It is tempting to speculate that the hemispheric dissociation of alexia and prosopagnosia is a specific consequence of a more general dissociation in the processing of contrast information by the two hemispheres, with the right hemisphere being more adequate to lay down exact face representations including information about contrast polarity.

In conclusion, our findings provide further evidence for the notion of a particular competence of the right hemisphere for visual attributes (Vandenbulcke, Peeters, Fannes, & Vandenberghe, 2006), in line with several neurobiological theories of knowledge processing for object recognition (e.g., Farah, 1990; Humphreys & Forde, 2000; Humphreys & Riddoch, 1984; Shallice, 1988; Warrington & McCarthy, 1987). In addition, our specific paradigm of testing pattern category learning in hemianopic patients with unilateral brain lesions adds a novel perspective by demonstrating a generic ability of the remaining intact (left or right) hemisphere to learn pattern categories with two very different sets of stimuli. Despite this apparently bi-hemispheric competence the underlying representations in each hemisphere differed qualitatively as evidenced by their different potential for generalization to contrast reversal. The results raise the possibility of a multiple (rather than unitary) representation of visual categories that could facilitate perceptual invariance and thereby improve the robustness of object recognition.

In our study we made use of the fact that, owing to the location and extent of the brain lesions in our patients, we could assess the contribution of the remaining intact left or right hemisphere in relative isolation. Future work could consider – based on single-case or neuroimaging paradigms – a complementary approach, in which categorization performance of the lesioned hemisphere is cross-referenced with regard to the location of the lesion and its associated visual field deficits. Similar to previous work in the domains of face recognition (e.g., Sorger, Goebel, Schiltz, & Rossion, 2007) and motion perception (e.g., Castelo-Branco et al., 2006) such a strategy could provide a route to explore within each hemisphere the functional neuroanatomy underlying visual category representations.

Acknowledgements

This study was supported by the Deutsche Forschungsgemeinschaft, grants Re 337/10-2, Re 337/12-1, to Ingo Rentschler, and by the Economic & Social Research Council, grant RES-062-0167, to Martin Jüttner. We are indebted to Dr. Roger Graves (Department of Psychology, University of Victoria, Canada) for his advice and help with regard to the statistical analysis of the data. We also thank PD Dr. Peter Brugger (Department of Neurology, University Hospital Zurich) and Prof. Avinoam Safran (Ophthalmology Clinic, Geneva University Hospital) for their support.

References

- Beaton, A., & Blakemore, C. (1981). The effects of contrast, stimulus duration, and spatial frequency on visible persistence in normal and specifically disabled readers. *Journal of Experimental Psychology: Human Perception & Performance*, 7, 495–505.
- Bruner, J. (1957). On perceptual readiness. *Psychological Review*, 64, 123–152.
- Campbell, R., Landis, T., & Regard, M. (1986). Face recognition and lipreading: A neurological dissociation. *Brain*, 109, 509–521.
- Castelo-Branco, M., Mendes, M., Silva, M. F., Januario, C., Machado, E., Pinto, A., Figueiredo, P., & Freire, A. (2006). Specific retinotopically based magnocellular impairment in a patient with medial visual dorsal stream damage. *Neuropsychologia*, 44, 238–253.
- Davidoff, J., & Warrington, E. K. (1999). The bare bones of object recognition: Implications from a case of object recognition impairment. *Neuropsychologia*, 37, 279–292.
- Davidoff, J., & Warrington, E. K. (2001). A particular difficulty in discriminating between mirror images. *Neuropsychologia*, 39, 1022–1036.
- De Renzi, E., Faglioni, P., & Spinnler, H. (1969). The performance of patients with unilateral brain damage on face recognition tasks. *Cortex*, 4, 17–34.
- Farah, M. (1990). *Visual agnosia*. Cambridge, MA: MIT Press.
- Galper, R. E. (1970). Recognition of faces in photographic negative. *Psychonomic Science*, 19, 207–208.
- Gauthier, I., Anderson, A., Tarr, M. J., Skudlarski, J., & Gore, J. (1997). Levels of categorization studied using functional magnetic resonance imaging. *Current Biology*, 7, 645–651.
- Goldberg, E., & Costa, L. D. (1981). Hemispheric differences in the acquisition and use of descriptive systems. *Brain and Language*, 14, 144–173.
- Grüsser, O. J., & Landis, T. (1991). Visual agnosia and other disturbances of visual perception and cognition. In J. R. Cronly-Dillon (Ed.), *Vision and visual dysfunction*. London: Macmillan Press.
- Hayes, A., Morrone, M. C., & Burr, D. C. (1986). Recognition of positive and negative bandpass-filtered images. *Perception*, 15, 595–602.
- Hécaen, H., & Angelergues, J. de. (1956). Agnosie visuelle pour les objets inanimés par lésion unilatérale gauche. *Revue Neurologique*, 94, 222–233.
- Hellige, J. B., & Michimata, C. (1989). Categorization versus distance: Hemispheric differences for processing spatial information. *Memory and Cognition*, 17, 770–776.
- Hoff, H., & Pözl, O. (1937). Über eine optisch-agnostische Störung des "Physiognomie-Gedächtnisses". *Zeitschrift für die gesamte Neurologie und Psychiatrie*, 159, 367–395.
- Humphreys, G. W., & Forde, E. M. E. (2000). Hierarchies, similarity and interactivity in object recognition. *Behavioral and Brain Sciences*, 24, 453–476.
- Humphreys, G. W., & Riddoch, M. J. (1984). Routes to object constancy: Implications from neurological impairments of object constancy. *Quarterly Journal of Experimental Psychology*, 36A, 385–415.
- Jager, G., & Postma, A. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: A review of the current evidence. *Neuropsychologia*, 41, 504–515.
- Jonides, J., Smith, E. E., Koeppe, R. R., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working memory in humans as revealed by PET. *Nature*, 363, 623–625.
- Jüttner, M., Langguth, B., & Rentschler, I. (2004). The impact of context on category learning and representation. *Visual Cognition*, 11, 921–945.
- Jüttner, M., & Rentschler, I. (1996). Reduced perceptual dimensionality in extrafoveal vision. *Vision Research*, 36, 1007–1021.
- Jüttner, M., & Rentschler, I. (2000). Scale invariant superiority of foveal vision in perceptual categorization. *European Journal of Neuroscience*, 12, 353–359.
- Jüttner, M., & Rentschler, I. (2008). Category learning induces position invariance of pattern recognition across the visual field. *Proceedings of the Royal Society B*, 275, 403–410.
- Kahana, M. J., & Bennett, P. J. (1994). Classification and perceived similarity of compound gratings that differ in relative spatial phase. *Perception & Psychophysics*, 55, 642–656.
- Kitterle, F. L., & Kaye, R. S. (1985). Hemispheric symmetry in contrast and orientation sensitivity. *Perception & Psychophysics*, 37, 391–396.
- Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C., Tang, J., & Gabrieli, J. D. E. (1989). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 723–735.
- Laeng, B., & Rouw, R. (2001). Canonical views of faces and the cerebral hemispheres. *Laterality*, 6, 193–224.
- Laeng, B., Zarrinpar, A., & Kosslyn, S. M. (2003). Do separate processes identify objects as exemplars versus members of basic-level categories? Evidence from hemispheric specialization. *Brain and Cognition*, 53, 15–27.
- Liu, C. H., & Chaudhuri, A. (1997). Face recognition with multi-tone and two-tone photographic negatives. *Perception*, 26, 1289–1296.
- Marsolek, C. J. (1995). Abstract visual-form representations in the left cerebral hemisphere. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 375–386.
- Marsolek, C. J. (1999). Dissociable neural subsystems underlie abstract and specific object recognition. *Psychological Science*, 10, 111–118.
- Marsolek, C. J., Kosslyn, S. M., & Squire, L. R. (1992). Form-specific visual priming in the right cerebral hemisphere. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 18, 492–508.
- Marsolek, C. J., Squire, L. R., Kosslyn, S. M., & Lulenski, M. E. (1994). Form-specific explicit and implicit memory in the right cerebral hemisphere. *Neuropsychology*, 8, 588–597.
- Marzi, C. A., & Berlucchi, G. (1977). Right visual field superiority for accuracy of recognition of famous faces in normals. *Neuropsychologia*, 15, 751–756.
- Marzi, C. A., Tassinari, G., Tressoldi, P. E., Barry, C., & Grabowska, A. (1985). Hemispheric asymmetry in face perception tasks of different cognitive requirement. *Human Neurobiology*, 4, 15–20.
- May, R., Hunter, M., & Gabriel, R. (1993). *NPFact 1.0*. Victoria, Canada: University of Victoria, Department of Psychology.
- Nederhauser, M., Yue, X., Mangini, M. C., & Biederman, I. (2007). The deleterious effect of contrast reversal on recognition is unique to faces, not objects. *Vision Research*, 47, 2134–2142.
- Notman, L. A., Sowden, P. T., & Özgen, E. (2005). The nature of learned categorical perception effects: A psychophysical approach. *Cognition*, 95, B1–B14.

- Peterzell, D. H., Harvey, L. O., Jr, & Hardyck, C. D. (1989). Spatial frequencies and the cerebral hemispheres: Contrast sensitivity, visible persistence, and letter classification. *Perception & Psychophysics*, *46*, 443–455.
- Posner, M. I., & Keele, S. W. (1968). On the genesis of abstract ideas. *Journal of Experimental Psychology*, *77*, 353–363.
- Prabhakaran, V., Smith, J. A., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1997). Neural substrates of fluid reasoning: An fMRI study of neocortical activation during performance of Raven's progressive matrices test. *Cognitive Psychology*, *33*, 43–63.
- Rao, S. M., Rourke, D., & Whitman, R. (1981). Spatio-temporal discrimination of frequency in the right and left visual field: A preliminary report. *Perceptual & Motor Skills*, *53*, 311–316.
- Rentschler, I., & Jüttner, M. (2007). Mirror-image relations in category learning. *Visual Cognition*, *15*, 211–237.
- Rentschler, I., Jüttner, M., & Caelli, T. (1994). Probabilistic analysis of human supervised learning and classification. *Vision Research*, *34*, 669–687.
- Rosch, E. (1978). Principles of categorization. In E. Rosch, & B. Lloyd (Eds.), *Cognition and Categorization* (pp. 27–48). Hillsdale, NJ: Erlbaum.
- Rybash, J. M., & Hoyer, W. J. (1992). Hemispheric specialization for categorical and coordinate spatial representations: A reappraisal. *Memory and Cognition*, *20*, 271–276.
- Scheidler, W., Landis, T., Rentschler, I., Regard, M., Encke, W., & Baumgartner, G. (1992). A pattern recognition approach to visual agnosia. *Clinical Vision Sciences*, *7*, 175–193.
- Seger, C. A., Poldrack, R. A., Prabhakaran, V., Zhao, M., Glover, G. H., & Gabrieli, J. D. E. (2000). Hemispheric asymmetries and individual differences in visual concept learning as measured by functional MRI. *Neuropsychologia*, *38*, 1316–1324.
- Shallice, T. (1988). *From neuropsychology to mental structure*. New York: Cambridge University Press.
- Silva, M. F., Maia-Lopes, S., Mateus, C., Guerreiro, M., Sampaio, J., Faria, P., & Castelo-Branco, M. (2008). Retinal and cortical patterns of spatial anisotropy in contrast sensitivity tasks. *Vision Research*, *48*, 127–135.
- Smith, E. E., & Jonides, J. (1997). Working memory: A view from neuroimaging. *Cognitive Psychology*, *33*, 5–42.
- Sorger, B., Goebel, R., Schiltz, C., & Rossion, B. (2007). Understanding the functional neuroanatomy of acquired prosopagnosia. *Neuroimage*, *35*, 836–852.
- Squire, L. R., & Knowlton, B. (1995). Learning about categories in the absence of memory. *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 12470–12474.
- Subramaniam, S., & Biederman, I. (1997). Does contrast reversal affect object recognition. *Investigative Ophthalmology and Visual Science*, *38*, 998.
- Vandenbulcke, M., Peeters, R., Fannes, K., & Vandenberghe, R. (2006). Knowledge of visual attributes in the right hemisphere. *Nature Neuroscience*, *9*, 964–970.
- Warrington, E. K., & McCarthy, R. (1987). Categories of knowledge: Further fractionations and an attempted integration. *Brain*, *110*, 1273–1296.
- Warrington, E. K., & Taylor, A. M. (1973). The contribution of the right parietal lobe to object recognition. *Cortex*, *9*, 152–164.
- Warrington, E. K., & Taylor, A. M. (1978). Two categorical stages of object recognition. *Perception*, *7*, 695–705.
- Wharton, C. M., & Grafman, J. (1998). Deductive reasoning and the brain. *Trends in Cognitive Sciences*, *2*, 54–59.
- Zihl, J., Cramon, & von, D. (1985). Visual field recovery from scotoma in patients with postgeniculate damage: A review of 55 cases. *Brain*, *108*, 335–365.