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Complementary deficits in perceptual classification in pure alexia and acquired prosopagnosia – new insights from two classic cases

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Abstract

Pure alexia and prosopagnosia traditionally have been seen as prime examples of dissociated, category-specific agnosias affecting reading and face recognition, respectively. More recent accounts have moved towards domain-independent explanations that postulate potential cross-links between different types of visual agnosia. According to one proposal, abnormal crowding, i.e. the impairment of recognition when features of adjacent objects are positioned too closely to each other, might provide a unified account for the perceptual deficits experienced by an agnosic patient. An alternative approach is based on the notion of complementary visual subsystems favouring the processing of abstract categories and specific exemplars, respectively. To test predictions of these two approaches with regard to pure alexia and prosopagnosia, we present previously unpublished data on digit recognition and visual crowding from two in the neuropsychological literature extensively studied patients, KD and MT (e.g., Campbell et al., 1986; Landis and Regard, 1988; Rentschler et al., 1994). Patient MT, diagnosed with pure alexia, showed pronounced abnormal foveal crowding, whereas KD, diagnosed with prosopagnosia, did not. These results form a distinct double dissociation with the performance of the two patients in other perceptual classification tasks involving Gabor micropatterns and textures as well as Glass patterns, which revealed a significantly greater impairment in KD relative to MT. Based on an analysis of the specific task demands we argue that prosopagnosia and pure alexia may involve complementary deficits in instantiation and abstraction, respectively, during perceptual classification, beyond any category specificity. Such an explanation appears in line with previous distinctions between a predominantly left-hemispheric, abstract-category and a predominantly right-hemispheric, specific-exemplar subsystem underlying object recognition.

Keywords: Prosopagnosia, alexia, perception, classification, categorization, crowding

1. Introduction

The term *visual agnosia* refers to a diverse class of neuropsychological disorders characterized by the inability to recognize familiar objects. Such failure occurs despite the agnosic individual exhibiting normal or near-normal elementary visual functions, such as acuity and contrast sensitivity, along with normal or near normal semantic and memory functions. Traditionally, two broad classes of agnosias have been distinguished: “apperceptive” agnosias, which comprise mainly perceptual processing deficiencies, and “associative” agnosias, which involve deficits either in the semantic knowledge of visual objects or in accessing such knowledge (Lissauer, 1890). Both classes include a wide range of more specific deficits ranging from the mild to the severe. Within the class of apperceptive agnosias further distinctions have been made, for example, between disorders affecting the discrimination of simple geometric shapes (shape/form agnosia; e.g. Milner et al., 1991; Riddoch et al., 2008), the recognition of familiar objects from unusual perspectives (transformational agnosia; e.g. Warrington, 1982), or the integration of local elements into a global shape (integrative agnosia; e.g., Riddoch and Humphreys, 1987). Associative agnosias include as an important subclass category-specific disorders that may affect the recognition of faces (prosopagnosia), words (alexia) or visually presented objects in general (visual object agnosia), despite intact perception of such stimuli (typically demonstrated by a preserved ability to copy them).

Given the diversity of dissociable visual disorders subsumed under the label *agnosia*, more recently there have been renewed attempts to establish cross-links between the associated patterns of impairments, in order to pinpoint the mechanisms underlying object recognition and their cortical implementation. With regard to apperceptive agnosias, Strappini et al. (2017) suggested that abnormal visual crowding in the central visual field might provide a unified account for the observed deficits. The phenomenon of crowding refers to an impairment of recognition when features of adjacent objects are positioned too closely to each other (Stuart and Burian, 1962). Crowding occurs for all types of stimuli and is most noticeable, in normal observers, in peripheral vision even though it affects pattern recognition across the whole visual field (for reviews, see Strasburger, 2020; Levi and Whitney, 2011; Strasburger et al., 2011). In a meta-analysis, Strappini et al. (2017) analysed the published data of 46 apperceptive agnosia patients for a range of standard visual-object-recognition tests that were either susceptible to crowding (complex-display tasks, e.g. triple-letter identification) or immune to it (simple-display tasks, e.g. the identification of simple geometric shapes or letters). For each patient and each test, they also experimentally determined the so-called equivalent eccentricity, i.e. the eccentricity at which peripheral vision of a normal (“standard”) observer was equivalent to central, i.e. foveal, vision of the agnosic patient. Strappini et al. found that for a given patient the equivalent eccentricities obtained for the different complex-display tests tended to coalesce around a single value, suggesting a conservation of critical eccentricity across those tests. While the exact neuroanatomical substrate underlying crowding is still unknown, psychophysical and fMRI studies indicate a cortical locus, with localisations varying between V1 and V4/V8 (e.g., Anderson et al., 2012; Levi, 2008; Fang and He, 2008; Freeman and Simoncelli, 2011; Gori and Spillmann, 2010; Millin et al., 2013). Based on the hypothesis that crowding in peripheral vision is determined by neural density, i.e. the number of neurons in the crowding-relevant cortical area (e.g. Pelli, 2008), Strappini et al. proposed that a similar factor might account for the various deficits exhibited in complex-display tasks by an agnosic patient. This factor could be described as abnormal crowding in central vision and reflect the reduced neural density in the (damaged) crowding-relevant cortical area of the agnosic observer.

There have been very few attempts to explore to what extent the abnormal-crowding hypothesis also provides a domain-independent explanation for the deficits observed in associative agnosia. In the one known study, Sand et al. (2018) tested four patients with associative, category-specific agnosia for abnormal crowding in central vision. Two patients had been diagnosed with pure alexia, the other two with acquired prosopagnosia. Foveal crowding was assessed using Pelli et al.'s (2016) critical spacing test. The test involves texture-like displays consisting of two alternating digits or letters. Size and spacing of these symbols are varied but maintain a fixed ratio, and the observer has to identify the two target symbols in the display. Visual crowding is assessed in terms of the so-called critical spacing between the targets, i.e. the minimum spacing required to achieve an identification performance at a pre-set criterion level. Using this procedure, Sand et al. found that only the two prosopagnosic patients showed foveal crowding that significantly differed from that obtained for a control group of healthy individuals. For the two alexic patients, however, there were no significant effects suggesting that abnormal crowding could not account for their category-specific deficit.

In contrast to the idea of a domain-independent explanation of pure alexia and prosopagnosia, it has long been hypothesized that these forms of associative agnosia might reflect impairments of separate subsystems underlying object recognition. Based on the typical dissociation pattern of associative agnosias, Farah (1991, 2004) distinguished between two systems of visual representations: one system that is primarily based on part-based object descriptions and used in particular for printed word recognition; the other system involves holistic representations (i.e., these are not analysed in terms of their parts) and is necessary in particular for the recognition of faces. According to Farah, the recognition of other object classes may recruit one or the other system, depending on the complexity of the objects and task requirements. Damage of the part-based system, typically based in the left occipito-temporal cortex, will result in alexia, and potentially object agnosia for objects with a well-defined part structure, while preserving the recognition of faces; damage of the holistic system, typically based in the right-occipito temporal cortex, will result in prosopagnosia, and potentially object agnosia for objects without a clear-cut part structure, but preserve the ability to read. Thus, Farah's two-system approach captures the dissociation patterns usually observed for pure alexia, prosopagnosia, and object agnosia.

More recently, a different, but potentially related characterization of the visual subsystems affected in associative visual agnosia has been suggested by McMenamin et al. (2015). It is based on an earlier model by Marsolek (e.g., Marsolek, 1995, 1999; Marsolek and Burgund, 2008) that - motivated mainly by repetition-priming experiments using divided field presentations - postulates a lateralized memory representation for visual objects. According to the model, visual forms are stored in the right hemisphere within a so-called *specific-exemplar* subsystem, whereas such forms are stored in the left hemisphere 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. More specifically, abstract-category recognition should rely on an assessment of independent features or dimensions, which may involve explicit rules and permit the storage of category-invariant features while disregarding within-category variability in object shape. This facilitates the mapping of different exemplars to the same categorical representation. 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 preserves within-category variability and permits to map different exemplars to different representations.

Using fMRI in conjunction with multivariate pattern analysis techniques, McMenamin et al. found evidence for asymmetric repetition priming effects in occipito-temporal cortex, with stronger abstract-category priming in the left hemisphere and stronger specific-exemplar priming in the right hemisphere. While McMenamin et al's study involved normal observers their findings suggest potential cross-links to the neuropathology and symptomology observed in pure alexia and prosopagnosia. Patients with left hemispheric damage - typical in pure alexia - should be more impaired in object categorization tasks involving abstract-category processing, for example when reading printed text. Patients with right hemispheric damage - typical in prosopagnosia - should be more impeded in the processing of specific exemplars, for example when recognizing individual faces. McMenamin et al. therefore related their model to Farah's two-system approach, with the part-based system implicating abstract-category processing and the whole-based system implicating specific-exemplar processing.

Marsolek's (1995, 1999) model to some extent is also reminiscent of an earlier model by Warrington and Taylor (1978; see also Warrington, 2009), which postulates two lateralized categorical stages, a left-hemispheric system for semantic categorization augmented by a right-hemispheric system for perceptual categorization. Similar to Farah's account, Warrington and Taylor's model is explicitly driven by the requirements of high–level object-recognition - here for example the need to deal with unusual perspectives of three-dimensional objects (a perceptual categorization task in Warrington and Taylor's terminology). By contrast, Marsolek's approach is more general in scope as they predict abstract-category and specific-exemplar effects also in low-level perceptual classification tasks involving simpler stimulus material, thus providing an alternative domain-independent explanation of the deficits in visual agnosia. Specifically with regard to associative agnosia, the above effects should be complementary in alexic and prosopagnosic patients, with the former being more impaired in tasks involving abstract-category rather than specific-exemplar processing, and the latter showing the opposite pattern. Such a task-dependent complementarity contrasts with the predictions of the abnormal-crowding account, which only implies crowding-related performance differences between patients that may depend on task but are not systematically related to their specific agnosia.

In the present paper we test these hypotheses by considering previously unpublished data from two patients that have been extensively studied in the neuropsychological literature, KD - diagnosed with acquired prosopagnosia, and MT - diagnosed with pure alexia. The two patients showed similarly sited, but differently sided lesions, following strokes of the right (KD) and left (MT) posterior cerebral artery, and – except for the side of the lesion – displayed extremely similar clinical pictures of their primary ophthalmological and neurological symptoms (for case histories see Christen et al., 1985; Campbell et al., 1986; Landis et al., 1986; Landis and Regard, 1988; Davidoff and Landis, 1990; Grüsser and Landis, 1991; Rentschler et al., 1994). However, the two cases dissociated at the level of higher visual processing, where - beyond their diagnostic category-specific deficits - they revealed a remarkable complementarity in their patterns of impairments: With regard to faces, KD showed deficits in the recognition of facial expressive gestures but could lipread speech, whereas MT revealed the reverse pattern (Campbell et al., 1986). Furthermore, KD had no problem in reading handwritten text, but was unable to identify the author of handwriting familiar to her. By contrast, MT could identify the author of familiar handwriting but was unable to read the written words (Landis and Regard, 1988).

Here we will report new data of KD and MT on letter recognition thresholds and foveal crowding which, collected already in 1994, have not been published before. We will contrast them with data from other tasks that assessed the performance of KD and MT in the perceptual classification of unfamiliar stimuli, namely Gabor micropatterns and textures, as well as Glass patterns (part of those data were published in Rentschler et al., 1994). In conjunction with the plethora of earlier findings for KD and MT outlined above, the new data offer a unique opportunity to pitch predictions of the abnormal-crowding account of visual agnosia against those based on the notion of separate subsystems for abstract-category and specific-exemplar processing.

2. Method

2.1 Subjects

The case histories, including CT scans, of patients KD and MT are well documented (Christen et al., 1985; Campbell et al., 1986; Landis et al., 1986; Landis and Regard, 1988; Davidoff and Landis, 1990; Grüsser and Landis, 1991). Both were out-patients at the Neurological University Hospital in Zurich, Switzerland. The assessments described in this paper were conducted at the Institute of Medical

Psychology, University of Munich, Germany. Informed consent from both patients was obtained and the study was conducted according the ethical standards laid down in the Declaration of Helsinki II.

In the following we will provide short summaries for each patient. Some key information and the clinical status of the two patients at the time of testing in the experiments reported in this paper are summarised in Table 1.

Table 1. Summary of the clinical and neuropsychological status of the patients KD and MT at the time of testing in 1994 (after Rentschler et al. 1994).

Patient	KD	MT
Details/ clinical history	Right-handed secretary, known hypertension (1 yr)	Right-handed housewife, uneventful medical history
Lesion	Right posterior cerebral artery stroke in 1981 at age 61	Left posterior cerebral artery stroke in 1984 at age 64
Localisation of Lesion	CT: large right medial temporo-occipital hypodensity including fusiform, lingual and posterior parahippocampal gyrus	CT: Large left medial occipito-temporal hypodensity including fusiform, lingual and posterior parahippocampal gyrus
Visual field defects	Left homonymous hemianopia (partial recovery of the lower left quadrant)	Right homonymous hemianopia
Visual acuity (decimal notation)	0.7-0.8	0.9-1.0
Neuropsychological status	Dense and persistent prosopagnosia; initially topographagnosia; impaired memory for non-verbal material, relatively spared memory for verbal material; identification of familiar handwriting impaired; lipreading intact; episodes of visual pseudo-hallucinations; mood depressed	Pure alexia, initially global, recovered to letter-by-letter reading; colour anomia; impaired memory for verbal material, relatively spared memory for non-verbal material; intact identification of familiar handwriting; lipreading impaired; mood unchanged

Patient KD

After admission to hospital in 1981 following a stroke at the age of 61, KD on neurological examination initially was found to have an incomplete left homonymous hemianopia. A CT scan showed an infarction in the territory of the right posterior cerebral artery. In the neuropsychological assessment, she showed a pronounced right posterior parietal syndrome with persisting prosopagnosia, topographical amnesia, loss of environmental familiarity, impaired revisualization, and impaired nonverbal learning and memory. Except for her slow reading on first testing, her language functions were completely intact.

KD continued to be closely investigated during the following years (for details, see Christen et al, 1985; Landis et al., 1986). Three years after her stroke, her hemianopia had receded to a left homonymous upper quadrantanopia, extending partly into the lower quadrant. The remainder of the neurological examination was normal. Her initial topographical amnesia also subsided but there was persisting loss of environmental familiarity. She regained the ability to visualize faces of family members or familiar places. She continued to be impaired, as she had been since her stroke, at identifying handwriting, including her own (Landis and Regard, 1988).

With regard to her face processing deficits, KD continued to be completely unable to recognize familiar people by their face. While her score in the Benton Facial Recognition Test fell into the low normal range she could not match facial profiles to schematic faces on the basis of facial expression, was poor at the recognition of famous people, and unable to sort face pictures for identity when given pictures of the same person at different ages. She was also uncertain when asked to sort face pictures on the basis of their sex. Furthermore, KD had difficulty categorizing facial expressions or generating such expressions on command. However, despite these problems with facial concepts she showed completely normal performance in lipreading (Campbell et al., 1986).

Patient MT

The patient was admitted to hospital in 1984 after a stroke at the age of 64. The neurological examination showed a right homonymous hemianopia, otherwise her neurological status was largely normal. A CT scan showed a left medial occipito-temporal hypodensity in the territory of the posterior cerebral artery. The neuropsychological assessment revealed a severe alexia without agraphia. Initially this extended to both single letter and word reading, but improved to a letter-by-letter word reading within two months. However, her letter reading remained slow. MT could recognize familiar handwriting regarding its author without being able to read it (Landis and Regard, 1988). She also showed a persistent colour anomia but could easily match and sort colours. For verbal learning, her immediate repetition span was normal but she revealed deficits in delayed recall. Her nonverbal learning and delayed recall were within the normal range. MT showed no aphasia, good verbal comprehension and repetition, and intact word naming for words presented orally, one letter at a time.

There was a mild naming defect for pictured complex actions but not for pictured simple objects, or parts of objects. MT had no difficulty in recognizing familiar faces, nor in sorting face pictures according to the sex of the face. She was unimpaired in categorizing facial expressions or generating them on demand. However, despite her competence with facial concepts she showed a clear impairment in lipreading (Campbell et al., 1986).

2.2 Apparatus

Stimulus patterns were generated as digital images with 8-bit grey levels on a TV monitor (Barco TVM 3/3.2, P4 phosphor), linked to a computer-controlled Videograph image processing system with 50 Hz frame rate (interlaced) and linear mapping between frame buffer content and display luminance (for details see Rentschler et al., 1988).

2.3 Stimuli and procedure

Contrast sensitivity thresholds. In order to determine the contrast-sensitivity function of each patient, sinusoidal gratings were generated as 128 x 128 pixel digital images. At a viewing distance of

123 cm the stimuli appeared under 2 x 2 deg of visual angle, with spatial frequencies at 1, 2, 4, 8, and 16 c/deg. Space average luminance of the patterns was set to 60 cd/m^2.

Contrast threshold were obtained by presenting stimulus pairs consisting of one vertical grating and a uniform grey background using a temporal two-alternative forced-choice (2AFC) procedure. Testing was binocular with an exposure duration of 1 s and an interstimulus interval of 700 ms. The observer had to indicate in which of the two intervals the grating had been presented. Threshold contrasts were computed using an adaptive psychophysical procedure with maximum likelihood estimation (ML-PEST; Harvey, 1986), with a 95% confidence interval of 0.2 log units. Typically between 20 and 40 trials were required to reach this accuracy level.

Character recognition thresholds. To assess character recognition thresholds in crowding and non-crowding viewing conditions, the stimuli and procedure of Strasburger et al. (1991) were used, except for a longer presentation time (200 ms) to ease the task for the patients. The stimuli were the 10 numeric characters 0 to 9, presented as white patterns on a grey background of 50 cd/m^2 (see illustration in Fig. 1). This setup permitted a maximum (Michelson) contrast of 46%. Each digit was specified within a 5 x 7 pixel matrix. Digit size was specified by digit height, thus the width of a digit equalled 0.71 times its size. In the Single Digit condition, the target digit was presented on its own. In the Crowding condition, the target digit was horizontally surrounded by two flanking digits. Target and flankers always were of the same size and contrast. The ratio of the spacing (midpoint-to-midpoint) between target and flankers to digit size *s* was kept constant at 1.4 (cf. Fig. 1).

Figure 1. Viewing conditions used to assess recognition thresholds for numeric characters. In the Single Digit condition (left) the target character was shown on its own. In the Crowding condition (right) the target digit was surrounded by two flanking characters of the same size and contrast. The ratio of distance *d* between target and flankers and digit size *s* was kept constant at 1.4. Characters are shown at an intermediate contrast for illustration purposes.

Contrast thresholds were obtained using a 10-alternative forced choice adaptive procedure. In each trial, a randomly chosen target digit (in the Crowding condition surrounded by flankers) was presented in the centre of the screen for 200 ms. The observer's task was to identify the target (in the Crowding condition the central character). Stimulus contrast was varied from trial to trial using Harvey's (1986) ML-PEST procedure until the 95% confidence interval of the threshold estimate reached a pre-specified level of 0.2 log units. Typically between 20 and 40 trials were required to reach this accuracy level.

At the minimum viewing distance of 44 cm the characters appeared at a size of 2 deg of visual angle. Character size was varied by changing viewing distance, covering a size range of 0.12 to 2 deg (in the case of KD) and 0.1 to 0.8 deg (in the case of MT). Testing proceeded from the largest to the smallest target size, and then in reverse order. Thus each target size was tested twice. The log contrast threshold data presented in the figures are the means of these descending and ascending series of trials.

Classification of Gabor micropatterns and textures. To study perceptual classification of unfamiliar stimuli, micropatterns were generated as compound Gabor gratings, resulting from the superposition of two sinewave gratings, a fundamental plus its third harmonic, within a Gaussian aperture. Such patterns have a well-defined one-dimensional part structure in terms of bright and dark bars along their horizontal symmetry axis. In the past, they have been used in numerous studies on visual categorization both in normal observers (e.g., Kahana and Bennett, 1994; Jüttner and Rentschler, 1996, 2000) and patients (Langguth et al., 2009). For the current experiments, the modulation frequencies of the fundamental and its third harmonic were set to 2 c/deg and 6 c/deg, respectively. Their maximum (Michelson) contrasts were set to 70% and 23%, respectively, with the luminance of the background set to 60 cd/m^2. While the fundamental was fixed in cosine phase, the phase angle of the third harmonic could be either 0 or 180 deg, resulting in two types of micropatterns with a distinctive single- or double-stripe structure (Fig. 2A). The micropatterns were generated as 32 x 32 pixel images, appearing at a size of 0.8 x 0.8 deg at the viewing distance of 80 cm. Gabor textures were constructed from 8 x 8 arrays of micropatterns. There were two types of nontarget (NT) textures and two types of target textures (T) (cf. Fig. 2B). The non-target textures consisted of 8 x 8 arrays of identical micropatterns (with either 0 deg or 180 deg phase); the target textures consisted either of a central array of 4 x 4 micropatterns of 0 deg phase surrounded by micropatterns of 180 deg phase, or vice versa (Fig. 2B). All texture stimuli were generated as 256 x 256 pixel images, appearing at a size of 6.2 x 6.2 deg at the viewing distance of 80 cm.

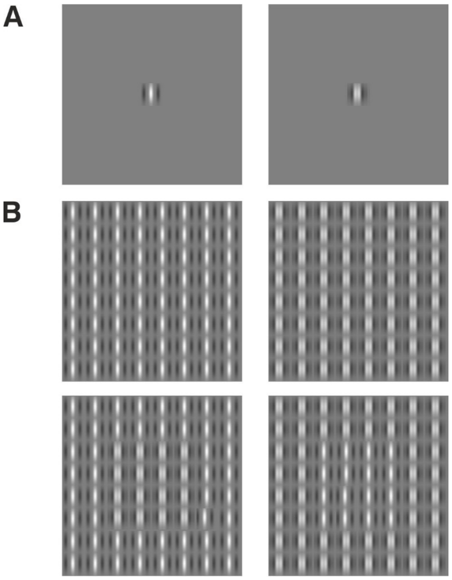

Figure 2. Gabor micropatterns and textures. (A) The micropatterns consisted of two superimposed grating patches, consisting of a fundamental and its third harmonic, added in 0 deg (peaks add) or 180 deg (peaks subtract) phase, resulting in a distinctive single or double-stripe structure. To measure discrimination, the patterns were presented in pairs either sequentially or simultaneously on a background of space average luminance. (B) To measure texture discrimination, the two micropatterns were combined into four types of texture pairs. Two of them were non-targets (top row), consisting of identical micropatterns in the centre and surround areas. The other two were targets (bottom row) consisting of the two different types of micropatterns in the centre and the surround areas.

Perceptual classification of the Gabor micropatterns was assessed in three viewing conditions: (1) Pairwise-Sequential, (2) Pairwise-Simultaneous, and (3) Texture. In the case of pairwise-sequential testing, the two patterns were displayed one by one in the screen centre for 120 ms, with an interstimulus interval of 700 ms. For pairwise-simultaneous testing, the two patterns were shown simultaneously above and below the screen centre (vertical centre-to-centre distance: 0.8 deg) for 120 ms. In either viewing condition, participants had to press one of six buttons on the keyboard to indicate their confidence that a pair of the same patterns (buttons l-3) or different patterns (buttons 4-6) had been presented. In the Texture condition, stimuli were presented one at a time with 120 msec exposure duration. Participants had to rate their confidence that a non-target (buttons 1-3) or target texture (buttons 4-6) had been presented. Each viewing condition comprised 50 target/different and 100 non-target/same trials. From the rating responses receiver operating characteristics (ROCs) were derived. Classification performance was evaluated in terms of the area under the ROC curve and its standard error, using a maximum likelihood solution (Dorfman and Alf, 1969). ROC area measures provide biasfree sensitivity estimates that are numerically equivalent to the proportion of correct responses in a 2-AFC paradigm, with values ranging from 0.5 to 1 (Green and Swets, 1974).

3. Results

3.1 Contrast sensitivity and recognition thresholds for numeric characters

Figure 3 shows the contrast thresholds for sinusoidal gratings, and numeric characters under non-crowding and crowding conditions, for the two patients. For sinusoidal gratings (Fig. 3A), both patients showed the typical U-shaped functions (inverted contrast sensitivity functions). Across the spatial frequency range of 1 to 8 cpd (no measurement was obtained at 16 cpd for KD), the two functions are almost congruent within the margins of measurement error.

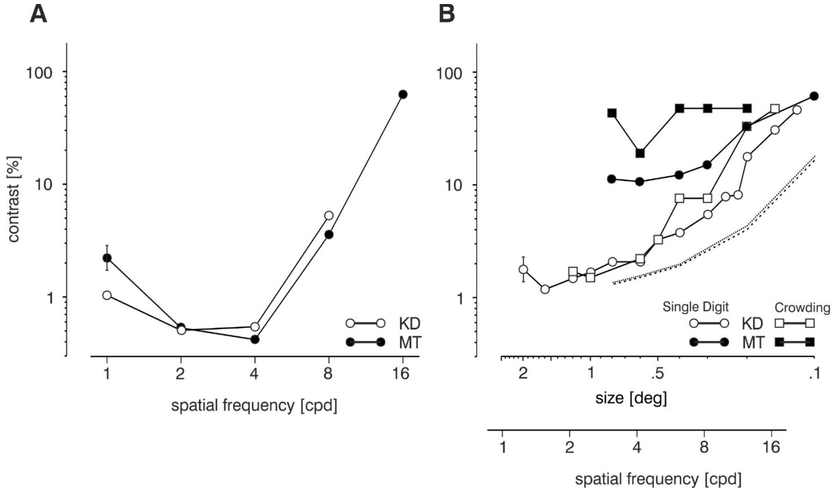

Figure 3. Contrast thresholds of KD and MT for sinusoidal gratings and numeric characters. (A) Detection thresholds for vertical, sinusoidal gratings as a function of spatial frequency. (B) Recognition thresholds for numeric characters as a function of letter size (solid lines). The range of equivalent spatial frequencies covered by the corresponding fundamental components is shown in a second abscissa. Target characters were presented either in isolation (Single Digit condition, circle symbols) or in the presence of flankers (Crowding condition, square symbols). For comparison, the data of a healthy control observer in the two conditions, taken from Strasburger et al. (1991; Fig. 5: subject MB) have been included (dashed lines). In each plot, error bars are provided only for one data point for sake of visual clarity. These error bars representative of the full data set and show 95% confidence limits of the threshold measurements.

For numeric characters, however, the data of the two patients reveal a distinct dissociation – despite, as illustrated in Figure 3, the similar range of spatial frequencies covered by the fundamental components of these patterns. For patient KD the contrast thresholds in the Single Digit and Crowding condition show a similar dependency on stimulus size, suggesting only a marginal effect of foveal crowding at the given target-flanker distance. As indicated in Figure 3B, the data of KD closely match that of a normal observer (subject MB, data replotted from Strasburger et al., 1991, Fig. 5) – taking into consideration KD's reduced visual acuity (cf. Table 1), which accounts for the horizontal offset between the two pairs of graphs.

A very different picture is evident in the data of patient MT. In the Single Digit condition her recognition thresholds are distinctly elevated relative to those of KD and the controls. This effect is even more pronounced in the Crowding condition, where MT's recognition thresholds for several stimulus sizes reach the maximum value of 47% (Michelson contrast) afforded by the luminance settings of the display. The dissociation between the two conditions indicates significant foveal crowding in MT. The fact that this dissociation is constrained by ceiling effects implies that the data shown in Fig. 3B represent a conservative estimate of the extent by which foveal crowding limits MT's recognition performance.

Our recognition task involved numeric characters, and it is well known that in many cases of pure alexia number reading tends to be less affected than letter identification and word reading (Starrfelt and Behrmann, 2011). While there is no evidence to suggest that MT's ability to read digits significantly differed from that to read non-numeric characters, the choice of digits as stimuli could be expected to make her task only easier. The pronounced impairment observed for the recognition of digits therefore also represents a conservative estimate for MT's decline in performance to be expected in the case of non-numeric characters.

To further quantify the extent of foveal crowding in the two patients, we derived estimates of the equivalent eccentricities, i.e. the eccentricity at which performance of a normal observer in peripheral vision would equate the performance of an agnosic patient in central vision, following the suggestion of Strappini et al. (2017). For this purpose we made use of the extensive data sets on contrast thresholds of numeric characters in direct and indirect view, and crowding and non-crowding conditions, provided in Strasburger et al. (1991) for normal observers, using the same stimulus material as in the current study. Visually matching the patient data against these reference data (Fig. 5 of Strasburger et al.) gave an equivalent eccentricity in the range of 2-4 deg in the case of KD, but 10-12 deg in the case of MT. These values should be seen as upper limits and may overestimate the actual ones, given the fact that the control observers were not age-matched to the patients.

In summary, the data on recognition thresholds show that, despite equivalent contrast sensitivity, the two patients show a pronounced dissociation with regard to their recognition thresholds for numeric characters, whether shown in isolation or in the presence of flankers. The recognition thresholds of the prosopagnosic patient closely match those of normal observers and showed only marginal evidence for foveal crowding – at least at the target-flanker distance used in the experiment. By contrast, the thresholds of the alexic patient appear distinctly elevated, signalling an impediment of recognition already present for single characters and distinctly further exacerbated by the presence of flanking characters, thus indicating significant foveal crowding.

3.2 Classification of Gabor micropatterns and textures

Figure 4 shows classification performance, in terms of the area under the ROC, for the two patients in the three viewing conditions. For each condition, the data of three normal observers (taken from Rentschler et al., 1988, Figs. 2 and 6[1]) have been added as a reference (solid circles). Patient KD shows a pronounced variability in her ability to discriminate between the Gabor micropatterns depending on viewing condition: In the case of a sequential presentation of the two patterns at the same retinal location, her performance is nearly perfect, matching that of the healthy controls. For a simultaneous presentation of the same patterns, however, her performance significantly deteriorates relative to that of the control group. Finally, when discriminating the same patterns embedded within a texture, her performance drops even further and approaches chance level.

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[1] Note that the data for normal observers in Figure 4 represent conservative estimates as these subjects were tested with a slightly smaller phase separation of 120 rather than 180 deg, which renders the discrimination marginally more difficult, see Rentschler et al. (1988).

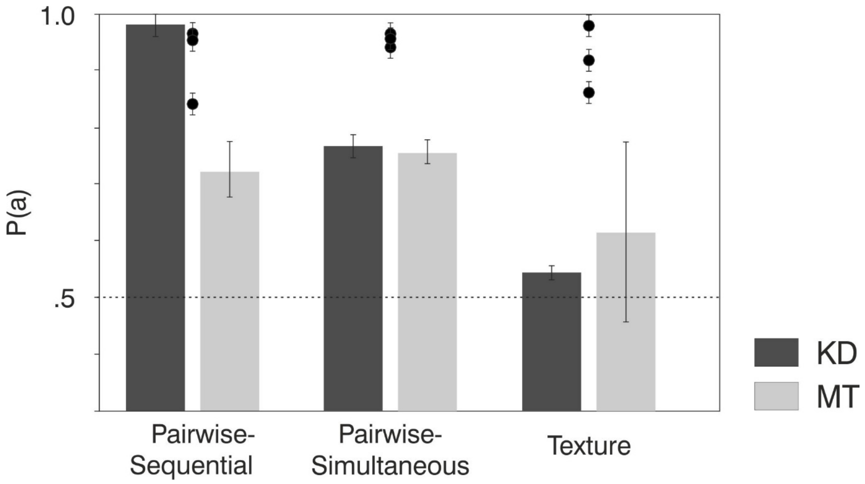

Figure 4. Classification performance of KD and MT for Gabor micropatterns and textures. Performance is shown in terms of *p*(*a*), the area under the ROC, under the three viewing conditions Pairwise-Sequential, Pairwise-Simultaneous, and Texture. For comparison, the data of three healthy control subjects, taken from Rentschler et al. (1988; Figs. 2 and 6), have been included (solid circles). The dashed line at *p*(*a*) = 0.5 indicates chance level. Error bars denote standard errors.

By contrast, classification performance of MT shows distinctly less variability with regard to a change in viewing condition. Her ability to discriminate between the pairs of micropatterns when shown simultaneously matches that of a sequential presentation. In both conditions, her performance is well above chance but significantly below that of healthy controls. In the Texture condition her discrimination performance indicates a slight drop even though the relatively large standard error in that condition prohibits a conclusion regarding the significance of that change. Overall, MT displays a distinctly reduced dependency of her performance on viewing condition compared to KD.

In summary, the classification data for Gabor micropatterns and textures show a further, distinct dissociation in the patterns of impairments of the two patients, both relative to each other and in comparison to healthy controls. While the latter have no problem to perform the classification task regardless of viewing condition, the prosopagnosic patient KD displays a pronounced dependency on how the patterns are presented, ranging from an almost perfect classification in the Sequential to a near-chance performance in the Texture condition. By contrast, the alexic patient MT displays a significantly reduced, but clearly above-chance, classification performance at a similar level across all three viewing conditions. In the following, we will consider possible explanations for these dissociations.

4. Discussion

In this paper we considered two domain-independent explanations for associative agnosias. According to the first one, abnormal crowding in the central visual field should present as a common deficit of visual agnosias (Strappini et al., 2017), regardless of the category-specific impairments typically used to define the individual disorders within that class. We tested this hypothesis by considering new data on digit recognition thresholds and foveal crowding obtained from two patients extensively studied in the neuropsychological literature, one of them diagnosed with acquired prosopagnosia (KD), the other with pure alexia (MT). Only one of them, MT, revealed significant foveal crowding. The other patient, KD, despite her severe prosopagnosic impairment only showed very marginal crowding in central vision and otherwise displayed a performance profile very similar to that of healthy controls. This suggests that abnormal foveal crowding may not provide a unified account for the deficits in prosopagnosia and pure alexia. Our results are partially supported by the findings of Sand et al. (2018), who also found evidence for abnormal foveal crowding in only some but not all of their four tested agnosic patients. Interestingly, in their study such crowding effects were only observed for the two prosopagnosic but not for the two alexic patients – a pattern of results complementary to that in our data. We will reconsider these differences and their possible explanation later in the discussion.

An alternative explanation for associative agnosias is provided by the hypothesis of separate subsystems for specific-exemplar and abstract-category processing of visual stimuli (McMenamin et al., 2015; Marsolek 1995; 1999). More specifically, it is assumed that the abstract-category subsystem relies on an assessment of independent stimulus features and dimensions and therefore facilitates an efficient representation of information common to input patterns belonging to the same class or category, while disregarding the within-category variability of its defining exemplars. Conversely, specific-exemplar recognition is thought to follow a more whole-based processing strategy, where features are represented in combination rather than independently. Such a strategy should maintain the identity of individual exemplars and thus facilitate their instantiation and subsequent discrimination, both within the same category and across different ones. Abstract-category and specific-exemplar subsystem therefore fulfil complementary functional roles reflecting the different requirements of basic- (or entry-)level and subordinate categorization, respectively, in object recognition (e.g. Rosch, 1978).

The two-subsystem approach predicts a domain-independent but task-dependent complementarity between the deficits observed in alexic and prosopagnosic patients, with the former being more impaired in abstract-category than specific-exemplar processing, and the latter showing the opposite pattern. In the current study, we tested these predictions in a range of perceptual classification tasks that systematically differed in their requirements concerning abstraction and instantiation. The recognition of low-contrast numeric characters required observers to match the sensory input to pre-existing, familiar stimulus categories (representing the numerals 0 – 9). This task could be accomplished by drawing primarily on abstract-category rather than specific-exemplar processing, as any within-category variation of the percepts due to the external noise in the visual input induced by the low-contrast presentation could be ignored. As predicted, the prosopagnosic patient KD performed very well in that task. She was also only minimally affected by the presence of flanker stimuli in the Crowding condition. By contrast, the alexic patient MT was expected to be more reliant on the specific features of the sensory input, i.e. the instantiation of adequate class exemplars, in order to compensate for the deficit in abstraction brought about by her pure alexia. This explains the higher susceptibility of that patient's performance to signal noise, i.e. her higher contrast thresholds, even in the Single Digit condition. MT's difficulties with instantiation were further exacerbated by the addition of flanker stimuli, as reflected in her distinctly declining performance in the Crowding condition.

The classification of Gabor micropatterns and textures imposed different demands on specific-exemplar and abstract-category processing. The unfamiliarity of the stimulus material implied that the same/different categorization required from the observer crucially relied on the instantiation of the two stimuli, i.e. the full representation of their specific features, to enable their comparison. While the discriminanda remained the same throughout the experiment, the three viewing conditions systematically manipulated the difficulty of that instantiation, and therefore the relative involvement of the specific-exemplar and abstract-category subsystem. In the condition involving a pairwise-sequential presentation of the two stimuli at the same retinal location, instantiation could be facilitated, if not partly by-passed, by using information retrieved from sensory memory and/or afterimages (as stimulus presentation was un-masked in our experiments). Thus a simple template-matching strategy may have been sufficient for a reliable same/different categorical response in that condition, thus imposing very little demand on an intact specific-exemplar processing. By contrast, instantiation in the Pairwise-Simultaneous condition was expected to be more demanding, requiring a proper encoding of the two stimuli in working memory. The abstract-category and specific-exemplar subsystem are assumed to achieve this aim in different ways. While the former relies on an analytical decomposition of the stimulus into parts and their relations, the latter is thought to be based on a more holistic strategy, representing the stimulus features in combination rather than separately. The ability to perform a same/different discrimination based on such stimulus representations may be partially preserved in the case of impairment of either the abstract-category or the specific-exemplar subsystem. Indeed there is evidence for such a dual processing of Gabor patterns in classification learning by patients with unilateral posterior lesions (Langguth et al., 2009). Finally, in the Texture condition the presence of additional distractors in the stimulus display could be expected to further impede the instantiation process, thus adding to the difficulty of the discrimination task. However, the analytical stimulus decomposition performed by the abstract-category subsystem necessitates the allocation of attention and may proceed more slowly than a holistic encoding (see Ashby and Maddox, 2005 and Hummel, 2001, for a discussion in the context of category learning and object recognition, respectively). Given the short presentation time, the impediment therefore could be expected to be more severe in the case of a discrimination based on abstract-category than on specific-exemplar processing.

The data for the classification of Gabor micropatterns of textures follow above predictions. The variation of the difficulty of the instantiation process from easy to difficult – and the corresponding variation in the reliance on specific-exemplar processing from low to high – is mirrored in the performance of the prosopagnosic patient KD. It ranges from a near-perfect classification in the case of the Pairwise-Sequential condition, at par with that of normal observers, to a performance level near chance in the Texture condition. Such a pattern is in line with the notion of an impaired specific-exemplar processing in that patient. By comparison, the performance of the alexic patient MT reveals much less variability. While MT's performance showed some impairment relative to control subjects across the three viewing conditions, her classification scores appear more robust against the varying demands on stimulus instantiation brought about by those conditions. This indicates that MT's problems are more related to the generation of a categorical (i.e., same vs. different) response, which is indicative for an impairment of her abstract-category subsystem.

Patient KD's particular difficulty with pattern discrimination in the Texture condition also offers an explanation for the finding of Sand et al (2018) regarding a foveal crowding effect in their prosopagnosic patients - a result that contrasts with the absence of such crowding for KD observed in our character recognition task. To assess foveal crowding, Sand et al. employed Pelli et al.'s (2016) critical spacing test, which involves texture-like displays consisting of two alternating digits or letters. Size and spacing of these symbols are varied but maintain a fixed ratio, and the observer has to identify the two target symbols in the display. Visual crowding is assessed in terms of the critical spacing between the targets, i.e. the minimum spacing required to achieve an identification performance at a pre-set criterion level. A correct response in this task requires both the instantiation of the two target characters within the texture, i.e. their processing as specific exemplars, and their categorization. Difficulties with the former (as illustrated in our study by KD in the case of Gabor textures) may therefore produce increases in the spacing thresholds, over and above any effects due to crowding. Such confounding effects may be further exacerbated in the case of particularly narrow and unfamiliar looking layouts for numeric symbols, as evident in the Pelli font employed by Sand et al. The increased spacing thresholds found in their prosopagnosic patients therefore may have reflected difficulties with specific-exemplar processing – in line with the findings of our study, rather than the effect of crowding alone.

In addition to KD's and MT's data for numeric character recognition and the classification of Gabor micropatterns and textures, the two-subsystem approach also provides an explanation of Rentschler et al.'s (1994) findings regarding the performance of the two patients in the seemingly rather different task of discriminating Glass patterns. In these experiments, the patients were presented with two-tone random dot patterns and transformed versions thereof (see e.g. Glass, 1969; Glass and Perez, 1973; Glass and Switkes, 1976). Based on a fixed prototype pattern, seven distorted versions were generated by randomly displacing each dot by a fixed absolute distance controlling the degree of the distortion. Glass patterns were obtained by superimposing a copy of the original pattern and a slightly rotated version of one of the seven perturbed versions (Fig. 5). The Glass patterns were shown one at a time for 120 msec. For each presentation, observers had to indicate, by pressing one of six buttons, whether they believed that a pattern with a pronounced (buttons l-3) or a weak (buttons 4-6) structure was being displayed. From the rating responses, ROCs were derived and classification performance was evaluated in terms of the area under the ROC curve, using the same technique as in the experiment assessing the classification of Gabor micropatterns and textures.

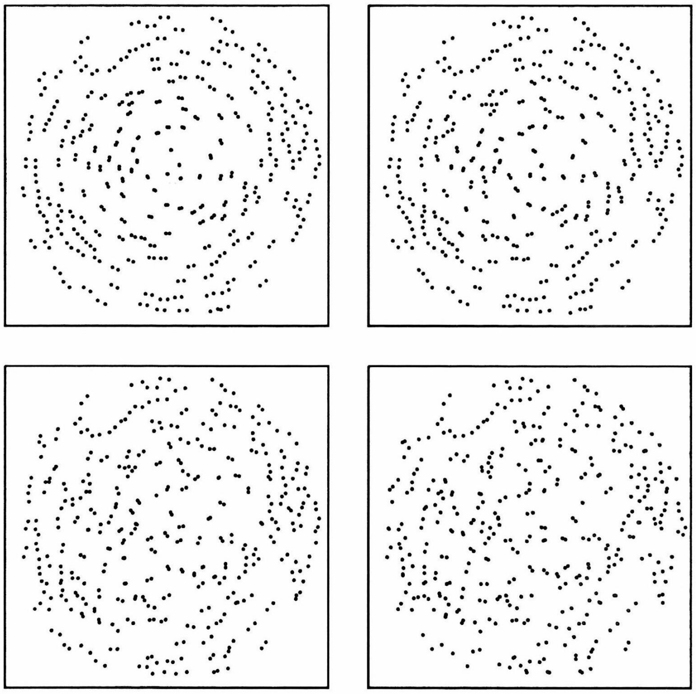

Figure 5. Glass patterns used by Rentschler et al. (1994). Based on a prototype pattern seven distorted versions were generated. For illustration, four of the seven stimulus patterns are shown, with zero, intermediate and maximum spatial distortion (from top left to bottom right; from Rentschler et al., 1994).

Figure 6 shows the psychometric curves of the two patients, i.e. their discrimination performance as a function of pattern distortion. For comparison, the data of two younger (aged 26 and 27) control observers (taken from Encke, 1990) are also shown. The alexic patient, MT, had no problem with detecting the gradually increasing perturbations applied to the original Glass pattern. Her performance mirrors that of the younger healthy controls except for a slight shift to higher distortion values at same performance level. By contrast, the prosopagnosic patient KD only succeeded to distinguish the most distorted versions of the Glass patterns from the (undistorted) original at a performance level above chance, suggesting an impaired ability to perceive Glass-like structures in the first place.

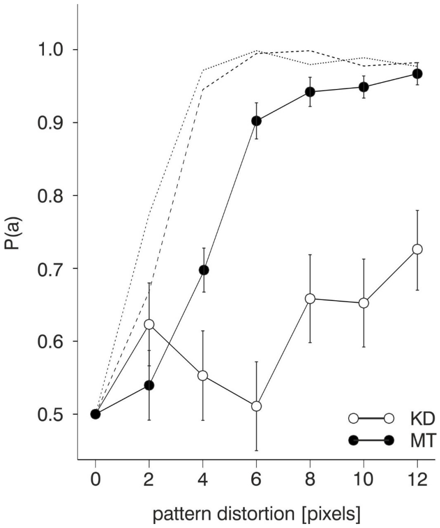

Figure 6. Discrimination performance of KD and MT for Glass patterns (after Rentschler et al., 1994). Performance is shown in terms of the area under the ROC as a function of pattern distortion. For comparison, the data of two healthy control subjects, taken from Encke (1990), have been added (dashed lines). Error bars denote standard errors.

The perceptual processing of Glass patterns is generally assumed to involve at least two stages: The first refers to the detection of local, parallel structures (here formed by the dipole-like pairs of dots), the second involves the integration of these oriented, local cues into a global form. Evidence from psychophysical (e.g. Wilson et al., 1997; Dakin, 1997) and neurophysiological (Smith et al., 2002, 2007) studies suggests that local orientation signals may be derived from the local image statistics in early visual cortex. While early visual areas may display some sensitivity also for global form aspects present in Glass patterns (Mannion et al. 2009, 2010) there is evidence that the pooling proper of local orientation signals into a global percept requires the involvement of higher cortical areas. For example, Ostwald et al (2008), using fMRI in conjunction with multivariate pattern analysis techniques, found evidence for such pooling in occipito-temporal cortex. More specifically, they observed a significantly higher selectivity for the *global* structure of Glass patterns in occipito-temporal areas that contrasted with an increased selectivity for elementary *local* features in early visual areas. Given the potential functional relevance of the occipitotemporal cortex for abstract-category and specific-exemplar processing (McMenamin et al., 2015), KD's difficulty with the perception of Glass patterns could be described again as a problem of incomplete instantiation, here manifesting itself in a reduced ability to integrate local pattern elements into a perceptual whole. Conversely, MT's intact instantiation implies a successful integration of the local dot pairs thus enabling her to perceive the global structure they form. Her slightly elevated discrimination threshold relative to that of healthy controls is compatible with the notion of an impaired abstract-category processing. It might result in a mild decline of performance even in the case of a simple rating task, even though the imperfect age matching between MT and the controls makes it more difficult to evaluate the extent of its impact.

As suggested by McMenamin et al. (2015), the notion of lateralised separate subsystems for specific exemplar and abstract category processing accounts for the category-specific deficits typically observed in prosopagnosia and pure alexia with regard to the recognition of familiar faces and reading printed text, respectively. In addition, it also provides an explanation of the more subtle deficits for these stimulus categories that have been reported for KD and MT in the literature. With regard to reading, Landis and Regard (1988) observed that KD had no problem in reading handwritten text, but was unable to identify the author of handwriting familiar to her. Conversely, MT could identify the author of familiar handwriting but was unable to read the written words. The double dissociation can be explained by noting that reading necessitates the decoding of written material regardless of stimulus attributes like letter shape and size, thus implying a dominance of abstract-category processing. By contrast, the identification of a person's handwriting relies on the precise representation of the geometric shape properties that reflect the idiosyncrasies of handwritten material, i.e., intact specific-exemplar processing. The double dissociation observed for KD and MT in those tasks, therefore, is in line with their deficits for specific-exemplar and abstract-category processing assumed to also underlie their prosopagnosia and pure alexia, respectively.

With regard to faces, Campbell et al. (1986) showed that KD, despite her severe prosopagnosia, was able to classify speech sounds by way of lipreading whereas she revealed deficits in the classification of facial expressive gestures, for example tongue protrusion and cheek puffing. By contrast, the alexic patient MT revealed the reverse pattern. Again, the two-subsystem approach offers an explanation of these dissociations, which have also been confirmed in more recent studies (e.g., Albonico and Barton, 2017). On the one hand, the mapping of lip movements to speech sounds constitutes – similar to reading – a highly practiced and automatized task, as the well-known McGurk effect (McGurk and Donald, 1976) - the perceived blending of seen and heard speech sounds that are not the same but presented in synchrony - demonstrates. This mapping involves categorical perception and therefore should mostly draw upon the abstract-category subsystem, thus benefitting KD relative to MT. Indeed Campbell et al. showed that KD was also susceptible to the McGurk effect to the same extent as were healthy controls, whereas the effect was absent in MT.

On the other hand, the facial gestures tested in the study (which did not include emotions) can be seen as less categorical in nature and to arise from a continuum of facial expressions. The classification of such gestures therefore should rely on a veridical representation of facial features and their metric configuration, i.e., their complete instantiation by the specific-exemplar subsystem. In that sense the double dissociation observed in the performance pattern for KD and MT again is compatible with the complementary impairments for abstract-category and specific-exemplar processing predicted by the respective disorder of each patient.

Finally, the two-subsystem approach offers an explanation for the more subtle impairments of object and face recognition demonstrated in KD by Landis and Davidoff (1991). They measured object- and face-superiority effects using the paradigm of Davidoff and Donnelly (1990). It requires the observer to recognize part changes in unfamiliar faces and non-face objects. Here normal observers show higher recognition performance for changes where the parts are embedded in the spatial context of a normal face or object, as opposed to scrambled versions thereof or when presenting the parts on their own – a phenomenon known as object/face superiority. Landis and Davidoff found that despite her clinically normal scores for the recognition of unfamiliar faces and non-face objects, KD did not show a superiority effect for either kind of stimulus. This indicates that her impairment extended beyond the defining deficit of her prosopagnosia, namely her inability to recognize familiar faces, into other stimulus domains. The two-subsystem approach accounts for such an overlap, as the putative impairment of the specific-exemplar subsystem in prosopagnosia may in principle manifest itself in more than one stimulus category, if that subsystem is invoked by a particular task. In the case of above paradigm, a deficit of the specific-exemplar system in the encoding of configural information specifying the spatial context of the target part may explain the absence of a facilitation to detect part changes within the context of both objects and faces.

6. Conclusions

In this paper we used new and existing data of two patients extensively studied in the neuropsychological literature to test predictions of two current domain-independent accounts for visual agnosia with regard to pure alexia and prosopagnosia. According to the first explanation, abnormal crowding in the central visual field should present as a common deficit of visual agnosias (Strappini et al., 2017), regardless of the type of any accompanying category-specific impairment. We found that only one of our patients (MT), diagnosed with pure alexia, revealed significant abnormal foveal crowding. For the other patient (KD), suffering from prosopagnosia, the extent of foveal crowding only minimally diverged from that of normal observers, rendering an explanation of her severe deficits in terms of such crowding unlikely. It should be noted that Strappini et al. based their abnormal-crowding hypothesis specifically on the data of patients suffering from apperceptive rather than associative forms of agnosia. However, this distinction appears blurred to some extent by the fact that in their study pure alexia (traditionally falling into the category of associative agnosias) was classified as an apperceptive disorder. Cases of explicit associative prosopagnosia were excluded but consideration was given to apperceptive prosopagnosia, defined by an additional impairment for recognizing visually similar stimuli other than faces – a criterion that patient KD in our study would also meet. Such ambiguity illustrates the problems of the quasi-dichotomous classification of visual agnosias, which dates back to Lissauer's (1890) distinction between impairments affecting the early perceptual processing on the one hand, and the activation of related memory representations on the other. Given the finding that many variants of visual agnosias tend to affect both of these stages to a varying extent, the now preferred concept is that of an apperceptive-associative continuum of visual disorders (Riddoch and Humphreys, 2003), or an agnosia spectrum (Behrman and Nishimura, 2010). Such a notion also appears more adequate given the diagnostic challenges raised by the apperceptive-associative distinction in the clinical practice (Grüsser and Landis, 1991). The two patients considered in our study, KD and MT, illustrate these complications. While both fulfil the clinical criteria of pure alexia and prosopagnosia, respectively, their problems clearly were not confined to associative deficits but rather became manifest – as demonstrated in the current paper - in a range of relatively low-level perceptual classification tasks. The distinct foveal crowding observed in MT is compatible with the idea that such crowding is closely associated with some form of dyslexic deficit (Crutch and Warrington, 2007). However, the causal relationship of early visual dysfunction and pure alexia remains controversial (Yong et al., 2013), and the absence of abnormal foveal crowding in the alexic patients examined by Sand et al. (2018) shows that such crowding may not be a necessary symptom of pure alexia. This suggests a limited generalisability of the crowding hypothesis and indicates that it may only account for a relatively small proportion of disorders on the agnosia spectrum.

A more comprehensive account of the various perceptual deficits shown by KD and MT is offered by the hypothesis of separate subsystems for abstract-category and specific-exemplar processing. Originally motivated by repetition-priming experiments using divided field presentations (e.g., Marsolek, 1995, 1999; Marsolek and Burgund, 2008) it postulates a lateralized memory representation for visual objects. According to the model, visual forms are stored in the right hemisphere within a so-called specific-exemplar subsystem, whereas in the left hemisphere such forms are stored within a so-called abstract-category subsystem. Unlike earlier models postulating lateralized object representations (Farah, 1991, 1994; Warrington and Taylor, 1978), which are driven mainly by the requirements of high–level object-recognition, Marsolek's account is more general in scope. As a consequence, it predicts abstract-category and specific-exemplar effects also in low-level perceptual classification tasks involving simpler stimuli. In the present study, the rare complementarity of KD and MT with regard to their lesion site in the left and right hemisphere, respectively, provides a unique opportunity to study the properties of the two subsystems in relative isolation. It allowed us to demonstrate that the two-subsystem approach offers a unified account of the deficits in the two patients in both low- and high-level tasks of visual classification and recognition.

Marsolek's two-subsystem approach predicts a relative (rather than absolute) hemispheric dominance. The notion of two subsystems for abstract-category and specific-exemplar processing therefore is compatible with the idea of a distributed and initially bilateral network that is being shaped by ontogenetic demands (Behrmann and Plaut, 2013, 2020). Behrmann and Plaut (2020) explain the lateralization of word and face processing as the result of a competition for neural space adjacent to retinotopic cortex areas, in particular in the ventral occipito-temporal (VOTC) regions in both hemispheres. As literacy is acquired, word recognition, which is co-lateralized with language, engages the left VOTC, leaving face recognition mediated primarily by the right VOTC. During development these regions are moulded further (Gomez et al., 2018; Nordt et al., 2019), morphing into the well-established visual word form area (VWFA; e.g. Cohen et al. 2000) and fusiform face area (FFA; e.g. Kanwisher et al., 1997), respectively. Based on our results we would like to speculate that these areas may represent focus points of two more extended systems with a broader functional specialisation, namely for the processing of abstract categories and specific exemplars. While the available pathologies of our two patients are broadly compatible with such an interpretation, we cannot know – given the diagnostic limitations at the time the patients were assessed – their distribution in sufficient detail to make further inferences about the neuro-functional architecture of these two systems. This question remains a topic for future research.

References

Albonico, A., Barton, J.J.S., 2017. Face perception in pure alexia: complementary contributions of the left fusiform gyrus to facial identity and facial speech processing. Cortex 96, 59-72.

Anderson, E.J., Dakin, S.C., Schwarzkopf, D.S., Rees, G., Greenwood, J.A., 2012. The neural correlates of crowding induced changes in appearance. Curr. Biol. 22, 1199 -1206.

Ashby, F.G., Maddox, W.T., 2005. Human category learning. Annu. Rev. Psych. 56, 149-178.

Behrmann, M., Nishimura, M., 2010. Agnosias. Wiley Interdiscip. Rev. Cogn. Sci. 1, 203-213.

Behrmann, M., Plaut, D.C., 2013. Distributed circuits, not circumscribed centers, mediate visual recognition. Trends Cogn. Sci. 17, 210-219.

Behrmann, M., Plaut, D.C., 2020. Hemispheric organization for visual object recognition: a theoretical account and empirical evidence. Perception 49, 373-404.

Campbell, R., Landis, T., Regard, M., 1986. Face recognition and lipreading. A neurological dissociation. Brain 109, 509-521.

Christen, L., Landis, T., Regard, M., 1985. Left hemispheric functional compensation in prosopagnosia? A tachistoscopic study with unilaterally lesioned patients. Hum. Neurobiol. 4, 9-14.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M.A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123: 291-307.

Crutch, S.J., Warrington, E.K., 2007. Foveal crowding in posterior cortical atrophy: A specific early-visual-processing deficit affecting word reading. Cog. Neuropsychol. 24, 843-866.

Dakin, S.C., 1997. The detection of structure in Glass patterns: psychophysics and computational models. Vision Res. 37, 2227–2246.

Davidoff, J., Donnelly, N., 1990. Object superiority: a comparison of complete and part probes. Acta Psychol. 73, 225–243.

Davidoff, J., Landis, T., 1990. Recognition of unfamiliar faces in prosopagnosia. Neuropsychologia 28, 1143-1161.

Dorfman, D.D., Alf Jr., E., 1969. Maximum likelihood estimation of parameters of signal detection theory and determination of confidence intervals-rating method data. J. Math. Psychol. 6, 487-496.

Encke, W. (1990). Moirémuster - experimentelle und theoretische Analyse eines Wahrnehmungsphänomens. Kyrill & Method, Munich.

Fang, F., He, S., 2008. Crowding alters the spatial distribution of attention modulation in human primary visual cortex. J. Vis. 8 (9), 6.

Farah, M.J., 1991. Patterns of co-occurrence among the associative agnosias: implications for visual object recognition. Cogn. Neuropsychol. 8, 1–19.

Farah, M.J., 2004. Visual agnosia, second ed. MIT Press, Cambridge (MA).

Freeman, J., Simoncelli, E.P., 2011. Metamers of the ventral stream. Nat. Neurosci. 14, 1195–1201.

Glass, L., 1969. Moiré effect from random dots. Nature 223, 578-580.

Glass, L., Perez, R., 1973. Perception of random dot interference patterns. Nature 246, 360-362.

Glass, L., Switkes, E., 1976. Pattern recognition in humans: Correlations which cannot be perceived. Perception 1, 67-72.

Gomez, J., Natu, V., Jeska, B., Barnett, M., Grill-Spector, K., 2018. Development differentially sculpts receptive fields across early and high-level human visual cortex. Nat. Commun. 9, 788.

Gori, S., Spillmann, L., 2010. Detection vs. grouping thresholds for elements differing in spacing, size and luminance. An alternative approach towards the psychophysics of Gestalten. Vision Res. 50, 1194–1202.

Green, D.M., Swets, J.A., 1974). Signal detection theory and psychophysics. Krieger, Huntington (N.Y.).

Grüsser, O. J., Landis, T., 1991. Visual agnosias and other disturbances of visual perception and cognition, in: Cronly-Dillon, J. R. (Ed.), Vision and Visual Dysfunction (Vol. 12). Macmillan Press, London.

Harvey Jr., L.O., 1986. Efficient estimation of sensory thresholds. Behav. Res. Methods Instrum. Comput. 18, 623-632.

Hummel, J.E., 2001. Complementary solutions to the binding problem in vision: implications for shape perception and object recognition. Vis. Cogn. 8, 489-517.

Jüttner, M., Rentschler, I., 1996. Reduced perceptual dimensionality in extrafoveal vision. Vision Res. 36, 1007-1021.

Jüttner, M., Rentschler, I., 2000. Scale invariant superiority of foveal vision in perceptual categorization. Eur. J. Neurosci. 12, 353-359.

Kahana, M.J., Bennett, P.J., 1994. Classification and perceived similarity of compound gratings that differ in relative spatial phase. Percept. Psychophys. 55, 642-656.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: A module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.

Landis, T., Regard, M., 1988. Hemianopsie und Agnosie. Klein. Monbl. Augenheilkd. 192, 525-528.

Landis, T., Cummings, J.L., Christen, L., Bogen, J.E., Imhof, H.G., 1986. Are unilateral right posterior cerebral lesions sufficient to cause prosopagnosia? Clinical and radiological findings in six additional patients. Cortex 22, 243-252.

Langguth, B., Jüttner, M., Landis, T., Regard, M., Rentschler, I., 2009. Differential impact of left and right hemisphere lesions on visual category learning and generalisation to contrast reversal. Neuropsychologia 47, 2927-2936.

Levi, D.M., 2008. Crowding-an essential bottleneck for object recognition: a mini-review. Vision Res. 48, 635–654.

Lissauer, H., 1890. Ein Fall von Seelenblindheit nebst einem Beitrage zur Theorie derselben. Arch. Psychiatr. Nervenkr. 21, 222 – 270.

Mannion, D.J., McDonald, J.S., Clifford C.W.G., 2009. Discrimination of the local orientation structure of spiral Glass patterns early in human visual cortex. Neuroimage 46, 511-515.

Mannion, D.J., McDonald, J.S., Clifford, C.W.G., 2010. The influence of global form on local orientation anisotropies in human visual cortex. Neuroimage 52, 600-605.

Marsolek, C.J., 1995. Abstract visual-form representations in the left cerebral hemisphere. J. Exp. Psychol. Hum. Percept. Perform. 21, 375-386.

Marsolek, C.J., 1999. Dissociable neural subsystems underlie abstract and specific object recognition. Psychol. Sci. 10, 111-118.

Marsolek, C.J., Burgund, E.D., 2008. Dissociable neural subsystems underlie visual working memory for abstract categories and specific exemplars. Cogn. Affect. Behav. Neurosci. 8, 17–24.

McGurk, H., MacDonald, J., 1976. Hearing lips and seeing voices. Nature 264, 746–748.

McMenamin, B.W., Deason, R.G., Steele, V.R., Koutstaaal, W., Marsolek, C.J., 2015. Separability of abstract-category and specific-exemplar visual object subsystems: evidence from fMRI pattern analysis. Brain Cogn. 93, 54-63.

Millin, R., Arman, A.C., Chung, S.T., Tjan, B.S., 2013. Visual crowding in V1. Cereb. Cortex 24, 3107-3115.

Milner, A.D., Perrett, D.I., Johnston, R.S., Benson, P.J., Jordan, T.R., Heeley, D.W., et al., 1991. Perception and action in "visual form agnosia". Brain 114, 405-428.

Nordt, M., Gomez, J., Natu, V., Jeska, B., Barnett, M., Grill-Spector, K., 2019. Learning to read increases the informativeness of distributed ventral temporal responses. Cereb. Cortex 29, 3124–3139.

Ostwald, D., Lam, J.M., Li, S., Kourtzi, Z., 2008. Neural coding of global form in the human visual cortex. J. Neurophysiol. 99, 2456-2469.

Pelli, D.G., 2008. Crowding: A cortical constraint on object recognition. Curr. Opin. Neurobiol. 18, 445-451.

Pelli, D.G., Waugh, S.J., Martelli, M., Crutch, S.J., Primativo, S., Yong, K.X., et al., 2016. A clinical test for visual crowding. F1000Res. 5, 81.

Rentschler, I., Hübner, M., Caelli, T., 1988. On the discrimination of compound Gabor signals and textures. Vision Res. 28, 279-291.

Rentschler, I., Treutwein, B., Landis, T., 1994. Dissociation of local and global processing in visual agnosia. Vision Res. 34, 963-971.

Riddoch, M.J., Johnston, R.A., Bracewell, R.M., Boutsen, L., Humphreys, G.W., 2008. Are faces special? A case of pure prosopagnosia. Cogn. Neuropsychol. 25, 3-26.

Riddoch, M.J., Humphreys, G.W., 1987. A case of integrative visual agnosia. Brain 110, 1431-1462.

Riddoch, M.J., Humphreys, G.W., 2003. Visual agnosia. Neurol. Clin. 21, 501 – 520.

Rosch, E., 1978. Principles of categorization, in: Rosch, E., Lloyd, B. (Eds.), Cognition and Categorization. Erlbaum, Hillsdale (NJ), pp. 27-48.

Sand, K., Robotham, R.J., Martelli, M., Starrfelt, R., 2018. Visual crowding in pure alexia and acquired prosopagnosia. Cogn. Neuropsychol. 35, 361-370.

Smith, M.A., Bair, W., Movshon, J.A., 2002. Signals in macaque striate cortex neurons that support the perception of Glass patterns. J. Neurosci. 22, 8334-8345.

Smith, M.A., Kohn, A., Movshon, J.A., 2007. Glass pattern responses in macaque V2 neurons. J. Vis. 7(3), 5.

Starrfelt R., Behrmann, M., 2011. Number reading in pure alexia - a review. Neuropsychologia 49, 2283-2298.

Strappini, F., Pelli, D.G., Di Pace, E., Martelli, M., 2017. Agnosic vision is like peripheral vision, which is limited by crowding. Cortex 89, 135–155.

Strasburger, H., 2020. Seven myths on crowding and peripheral vision. Perception 11, 1-46.

Strasburger, H., Harvey Jr., L.O., Rentschler, I., 1991. Contrast thresholds for identification of numeric characters in direct and eccentric view. Percept. Psychophys. 49, 495–508.

Strasburger, H., Rentschler, I., Jüttner, M., 2011. Peripheral vision and pattern recognition: a review. J. Vis. 11(5), 13.

Stuart, J.A., Burian, H.M., 1962. A study of separation difficulty: Its relationship to visual acuity in normal and amblyopic eyes. Am. J. Ophthalmol. 53, 471-477.

Warrington E.K., 1982. Neuropsychological studies of object recognition. Proc. R. Soc. Lond. Ser. B 298, 15–33.

Warrington, E.K., 2009. Two categorical stages of object recognition: A retrospective. Perception 38, 933-947.

Warrington, E.K., Taylor, A.M., 1978. Two categorical stages of object recognition. Perception 7, 695-705.

Whitney, D., Levi, D.M., 2011. Visual crowding: A fundamental limit on conscious perception and object recognition. Trends Cogn. Sci. 15, 160–168.

Wilson, H.R., Wilkinson, F., Asaad, W., 1997. Concentric orientation summation in human vision. Vision Res. 37, 2325-2330.

Yong, K.X., Warren, J.D., Warrington, E.K., Crutch, S.J., 2013. Intact reading in patients with profound early visual dysfunction. Cortex 49, 2294-2306.