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Impaired integration of object knowledge and visual input in a case
of ventral simultanagnosia with bilateral damage to area V4

E. Charles Leek¹, Giovanni d'Avossa¹, Marie-Josèphe Tainturier¹,
Daniel J. Roberts¹, Sung Lai Yuen², Mo Hu³ & Robert Rafal¹

¹ School of Psychology, Bangor University, Bangor, UK

² Institute for Systems Neuroscience, University Medical Center, Hamburg-Eppendorf, Germany

³ School of Medicine, Cardiff University, Cardiff, UK

Running Head: Overlapping figures and ventral simultanagnosia

Address for Correspondence

Charles Leek PhD

Wales Institute for Cognitive Neuroscience

School of Psychology

Bangor University

Bangor, Gwynedd, UK,

LL57 2AS

Tel: (+44) (0) 1248 382948

Email: e.c.leek@bangor.ac.uk

ABSTRACT

In this study we report some of the first evidence showing how brain-damage can affect the underlying processes that support the integration of sensory input and prior knowledge during the visual perception of shape. We report the case of patient MT with an acquired ventral simultanagnosia following posterior occipito-temporal lesions encompassing V4 bilaterally. Despite showing normal object recognition for single items, and intact low-level vision, MT was impaired in object identification with overlapping figures displays. Task performance was modulated by familiarity: unlike controls, MT was faster with overlapping displays of abstract shapes than common objects. His performance with overlapping common object displays was also influenced by both the semantic relatedness and visual similarity of the display items. These findings challenge claims that visual perception is driven solely by feedforward mechanisms, and show how brain-damage can selectively impair high-level perceptual processes supporting the integration of stored knowledge and visual sensory input.

Word Count: 150

Key words: Ventral simultanagnosia, perceptual integration, overlapping figures, V4

One of the fundamental issues in our understanding of human vision is the extent to which shape perception is driven solely by the rapid feedforward processing of sensory information, or is rather constrained by the integration of visual input with stored 'top-down' object knowledge. For example, evidence from EEG has shown that we are able to make rapid judgments about the presence of animals or non-animals in briefly presented scenes as quickly as 120-150ms following stimulus onset (Kirchner & Thorpe, 2006; Thorpe, Fize & Marlot, 1996; Fabre-Thorpe, Delorme, Marlot & Thorpe, 2001). Although the functional interpretation of these data have been questioned (e.g., Johnson & Olshausen, 2003), they have been taken as evidence in support of feedforward models of shape perception and object recognition (e.g., Riesenhuber & Poggio, 1999).

Alternatively, it has been proposed that shape perception is mediated by recurrent, interactive, processing dependent upon cortico-cortico feedback loops during both early and higher-levels of vision (Bar, 2003; Beck & Palmer, 2002; Fenske, Aminoff, Gronau & Bar, 2006; Freeman, Driver, Sagi & Zhaoping, 2003; Harel, Ullman, Harari & Bentin, 2011; Humphreys, Riddoch & Price, 1997; Ito & Gilbert, 1999; Lewicki & Sejnowski, 1997; Luck, Chelazzi, Hillyard & Desimone, 1997; Moran & Desimone, 1985; Peterson & Gibson, 1994; Rao & Ballard, 1999; Rock, 1962; Rolls, 2008; Schiller, 1993; Twomey, Kawabata Duncan, Price & Devlin, 2011).

Evidence of interactions between sensory input and prior knowledge during perception has been found in a variety of domains including, for example, attentional modulation of neuronal responses in early visual cortex (e.g., Ito & Gilbert, 1999; Luck et al., 1997; Moran & Desimone, 1985), letter identification and lexical access (e.g., McClelland & Rumelhart, 1981; Smith & Besner, 2001; Twomey et al., 2011), eye movement control during scene inspection (e.g., Foulsham & Underwood, 2007), and object grouping effects on visual crowding (Pelli, 2008; Saarela, Sayim, Westheimer & Herzog; 2009).

In this paper we present some of the first evidence from cognitive neuropsychology about how focal brain-damage can affect the processes underlying the high-level integration of visual input and object knowledge during shape perception. Patient MT suffered an ischemic stroke affecting the posterior and ventral occipital cortex bilaterally encompassing the fusiform gyri, V4, lingual gyri and (right) calcarine sulcus. Neuropsychological testing revealed prosopagnosia, letter-by-letter reading and difficulties in overlapping figures tasks – with no deficit in the perception and recognition of objects presented in isolation. Of particular interest was the pattern of normal and impaired performance he showed with overlapping figures.

In the standard version of the task, patients are presented with arrays of overlapping line drawings (Ghent, 1956; Poppelreuter, 1917). Responses can be measured in several

ways, including by asking patients to name individual objects, or to select items from a response sheet containing non-overlapping stimuli (Bisiach, Capitani, Nichelli & Spinnler, 1976; De Renzi, Scotti & Spinnler, 1969; Della Sala, Laiacona, Trivelli & Spinnler, 1995).

Successful performance requires accurate grouping and integration of image features belonging to different items occupying overlapping spatial locations. MT's performance was found to be strongly influenced by object familiarity: unlike controls, he did better with overlapping abstract shapes than with line drawings of familiar common objects. In addition, his performance with common objects was slower on displays containing items with high semantic relatedness and visual similarity (e.g., chicken, duck, rooster, ostrich) relative to displays with high visual (e.g., sun, orange, button, ring) or semantic (e.g., trumpet, piano, drum, guitar) similarity only. We argue that MT's impairment has affected high-level processes, mediated by extrastriate area V4, that support the integration of stored visual semantic object knowledge and sensory information during shape perception.

CASE REPORT

Background: Patient MT

MT is a right handed male who was 59 years old at time of testing. MT worked in a senior engineering capacity. He had no prior history of developmental abnormality, cognitive impairment or psychiatric condition. MT completed an undergraduate University degree in mathematics. Eight months prior to testing he was struck down at work with an acute headache and visual disturbance. Scanning revealed ischemic lesions affecting the posterior and ventral occipital cortex bilaterally encompassing the fusiform gyri, V4, lingual gyri and (right) calcarine sulcus – see Figure 1.

Upon admission to hospital he had a left inferior homonymous quadrantanopia (limited to the medial aspect of the quadrant), and full lower left achromatopsia – both of which had resolved by the time he was tested. MT's mini mental status examination score was 30/30 and he was able to give a cogent account of his personal history and current circumstances. Episodic memory was preserved. The remainder of his exam was normal, except for the visual disturbance detailed below. He had red-green achromatopsia, difficulties in face recognition, reading and in overlapping figures tasks (see Neuropsychology Assessment). Although he was able to recognize single objects, he

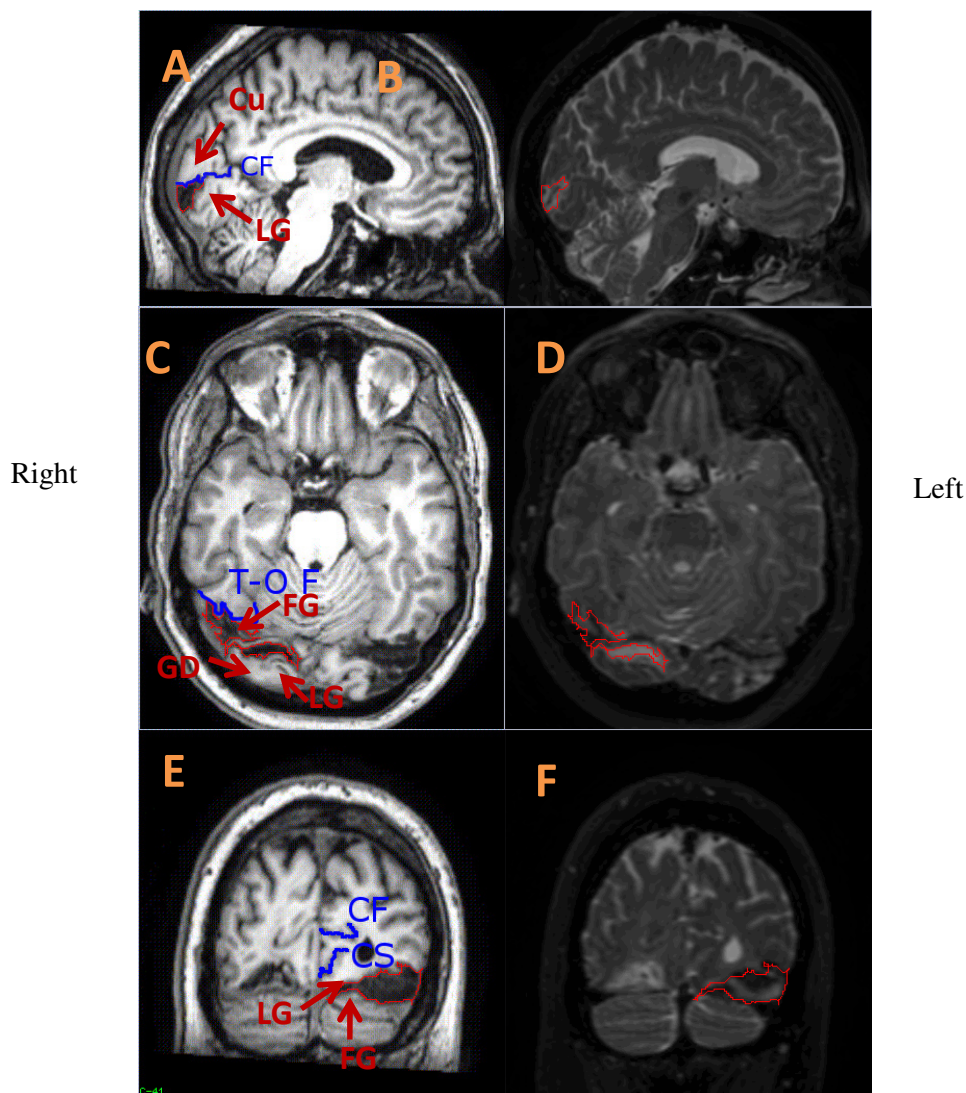


Figure 1. Lesion anatomy. Coregistered T1-weighted (panels A, C, and E) and T2-weighted images (panels B, D and F) show the location of the ischemic lesions in the occipital lobe. The anatomical boundaries of the three cortical strokes are outlined in red. Panel A and B show, in sagittal slices, the location of the stroke involving the right calcarine cortex. The axial slices in Panel C and D show the location of the parenchymal loss in the right, ventral occipital cortex. Finally, the coronal slices, in panel E and F, show the lesion affecting the left, ventral occipital cortex. Arrows highlight major gyral structures (Cu = cuneus, LG = lingual gyrus, FG = fusiform gyrus, GD = gyrus descendens) and blue lines delineate fissures or sulci (CF = calcarine fissure, T-OF = temporo-occipital fissure, CS = collateral sulcus).

described complex scenes in a piecemeal manner, reporting single details at a time. His overall clinical profile was consistent with ventral simultanagnosia with a transient achromatopsia and prosopagnosia (Duncan, Bundesen, Olsen et al., 2003; Farah, 1990).

Neuropsychological Assessment

A summary of MT's performance across a range of neuropsychological screening tests of visual perception, word reading, face perception and object recognition is shown in Table 1.

MT showed high verbal, performance and full IQ measures on the WAIS, and normal performance on all sub-tests of the CAMCOG (Roth, Tym, Mountjoy, Huppert, Hendrie, Verma & Goddard, 1986) which includes sub-tests for hemi-spatial neglect, basic orientation, language comprehension, memory, attention, ideo-motor praxis, calculation and visual reasoning. Object recognition was assessed using the 64-item picture naming task developed by Lambon Ralph, Howard, Nightingale & Ellis (1998). MT showed no impairment in either accuracy or naming latency. Further tests of his visual perception were performed using the Birmingham Object Recognition Battery (BORB: Riddoch & Humphreys, 1993). He showed normal performance in matching objects across changes in viewpoint (BORB Test 7), and was also within normal limits on the low-level vision tests of line length matching (Test 2), gap position (Test 5) and line orientation matching (Test 4) were within normal range. Additionally, MT performed at ceiling in copying the Rey Osterrieth figure – See Figure 2 (Osterrieth, 1944; Rey, 1941).

Table 1.

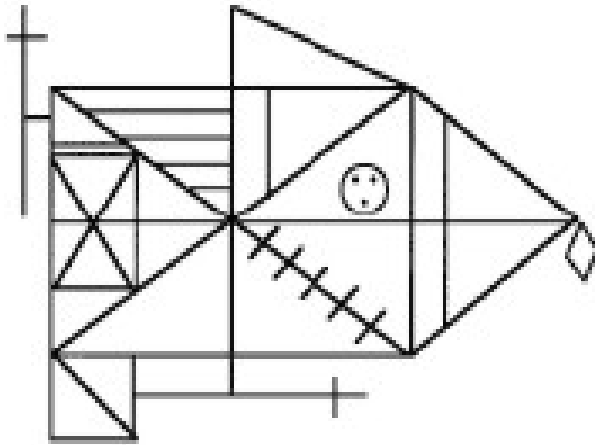
Summary of MT's performance during neuropsychological assessment.

		<u>MT</u>	
<u>General Cognitive Functioning</u>			
Wechsler Abbreviated Scale of Intelligence (WASI)	Full Scale IQ:	142	
	Verbal IQ:	139	
	Performance IQ:	135	
Cambridge Cognitive Examination (CAMCOG)		100/106	
<u>Reading & Writing</u>			
Timed single word reading: Word length effect (see Figure 3)			
Writing-to-dictation		30/30	
<u>Visual Object Recognition</u>			
	<u>MT</u>	<u>Controls</u>	
64 item picture naming task ¹	Accuracy	61/64 (95.31%)	M=97.2% (SD=5.52)
	RT	M=1068ms	M=1061ms (SD=153.57)
<u>Birmingham Object Recognition Battery²</u>			
Minimal Feature Match Task	25/25	Normal	
Gap Position Task	34/40	Range: 24-39	
Length Match Task	26/30	Range: 22-30	
Line Orientation Match Task	25/40	Range: 18-29	
Rey-Osterrieth Complex Figure (CFT)	32/32	Normal	
Famous Face Recognition	9/22	19-22	

¹ Lambon Ralph, Howard, Nightingale & Ellis (1998), control data supplied by Daniel Roberts.

² Control norms from the BORB (Riddoch & Humphreys, 1993): N = 39, age range 50-80).

(a) The Rey Figure



(b) MT's copy

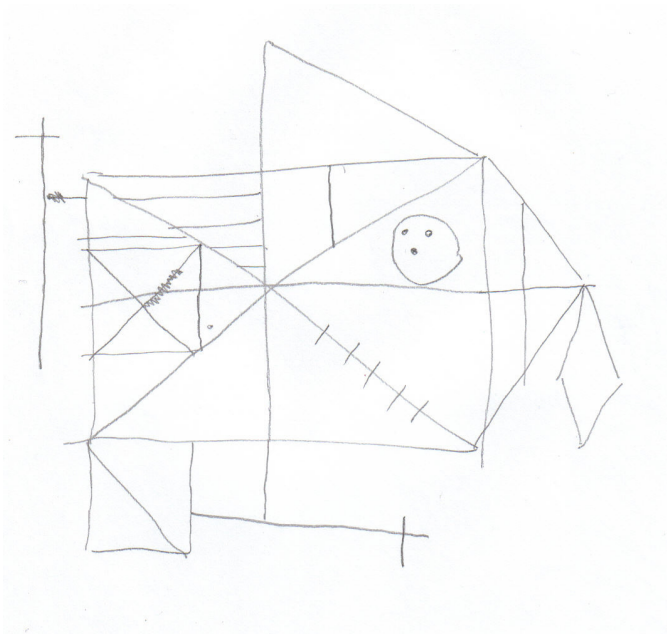


Figure 2 (a) Shows the original Rey Figure and (b) MT's copy.

In contrast, he showed a marked alexia without dysgraphia demonstrated by a word length effect in reading single words while performing at ceiling in writing to dictation (see Figure

3). The slope of MT's reading time was contrasted with that of 25 age-matched controls

using the modified t-test (Crawford & Garthwaite, 2002; Crawford, Garthwaite & Porter, 2010). This contrast was significant, $t = 39.22$, $p < .0001$. MT also performed poorly at identifying famous faces.

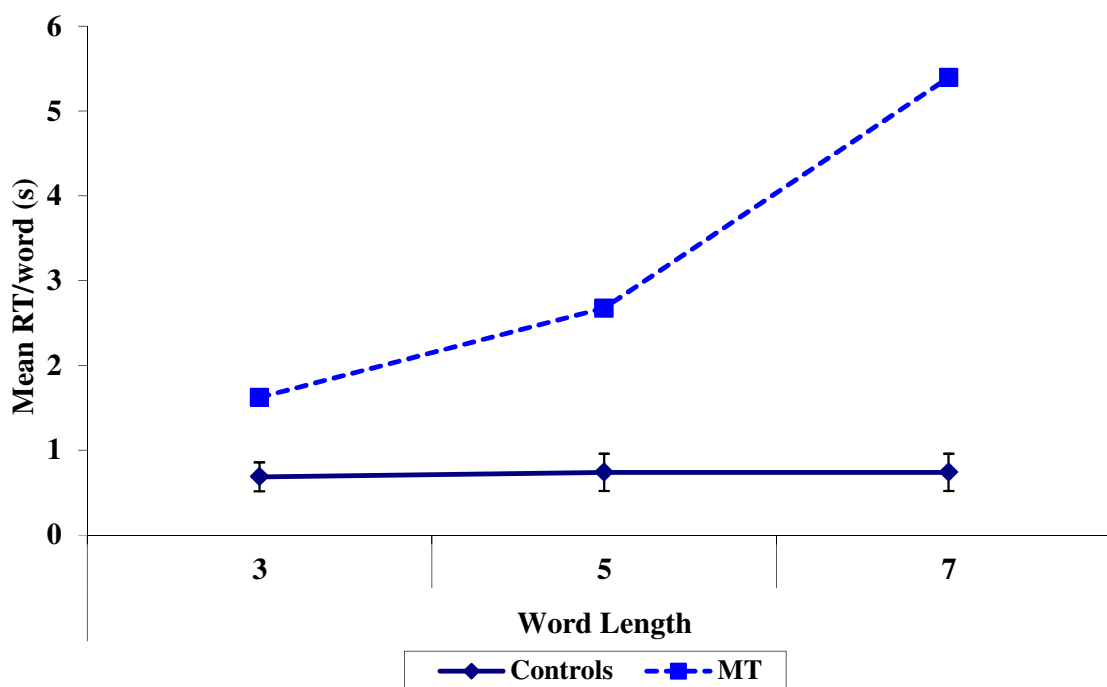


Figure 3 MT's performance on the word reading task (Mean s/word) relative to age-matched controls. Slopes reflect mean RTs as a function of word length ($t(8) = 39.22$; $p < .0001$). Bars show standard error.

MT's difficulties with overlapping figures tasks revealed during initial clinical examination highlight a potential deficit in perceptual integration. This was further assessed in the experimental investigation using a series of tests based on the Poppelreuter-Ghent Overlapping Figures Task (Ghent, 1956; Poppelreuter, 1917).

EXPERIMENTAL INVESTIGATION

METHODS

Control Subjects

A group of nine neurologically normal volunteers (aged 58-67, 5 female) served as controls. They were recruited from the Community Participant Panel of the School of Psychology, Bangor University. All subjects were right-handed, had normal or corrected-to-normal vision, and reported no previous history of psychiatric or neurological illness. Written informed consent was obtained. The controls completed all three overlapping figures tasks (see below) in a random order. Test procedures were identical for the controls and MT in all tests. Ethics approval for the study was granted from the University and local healthcare trusts. Informed consent was obtained from MT and all control participants, anonymity preserved in accordance with the Declaration of Helsinki (1991).

Stimuli, Design and Procedure

Task 1: Overlapping Figure Test 1(Common Objects)

The procedure was based on the method devised by Bisiach et al (1976). The participant is presented with an overlapping test display containing four superimposed line drawings (targets), and is then asked to point to the target items from a response display containing four non-overlapping targets and four distracters. This method avoids any requirement to make a verbal response. Line drawing stimuli were selected from the Snodgrass and

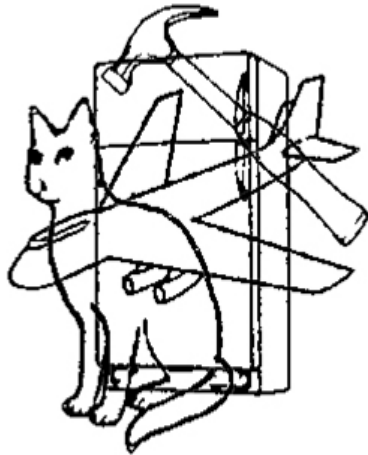
Vanderwart (1980) picture set.

Each test display contained four overlapping stimulus items - see Figure 4(a). There were eight overlapping display trials (32 overlapping stimuli) per condition in a 2 (Semantic Relatedness: High/Low) x 2 (Visual Similarity: High/Low) factorial design (N total overlapping display trials = 32; N total overlapping stimuli = 128):

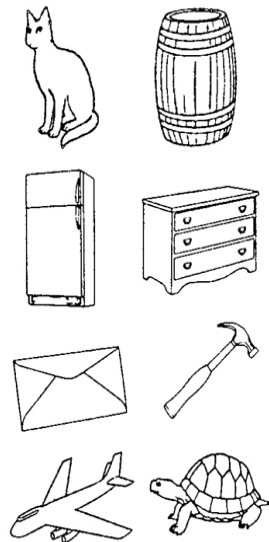
- (1) Semantic relatedness. Display items either consisted of stimuli with high semantic relatedness (e.g., piano, drum, guitar, trumpet) or low semantic relatedness (e.g., bear, scissors, sled, axe). In the high semantic relatedness displays all four overlapping items came from the same semantic category (e.g., musical instruments). In the low semantic relatedness displays the items came from different superordinate categories.
- (2) Visual similarity. Display items could be high (e.g., ring, button, orange, sun) or low (e.g., guitar, belt, apple, finger) in terms of the similarity of their global outline shapes. Items were classified in terms of the overall elongation and shape of the occluding contour regardless of orientation.

(a) **Overlapping common objects (Task 1)**

Display



Response Array



(b) **Overlapping abstract shapes (Task 2)**

Display



Response Array



(c) Non-overlapping control (Task 3)

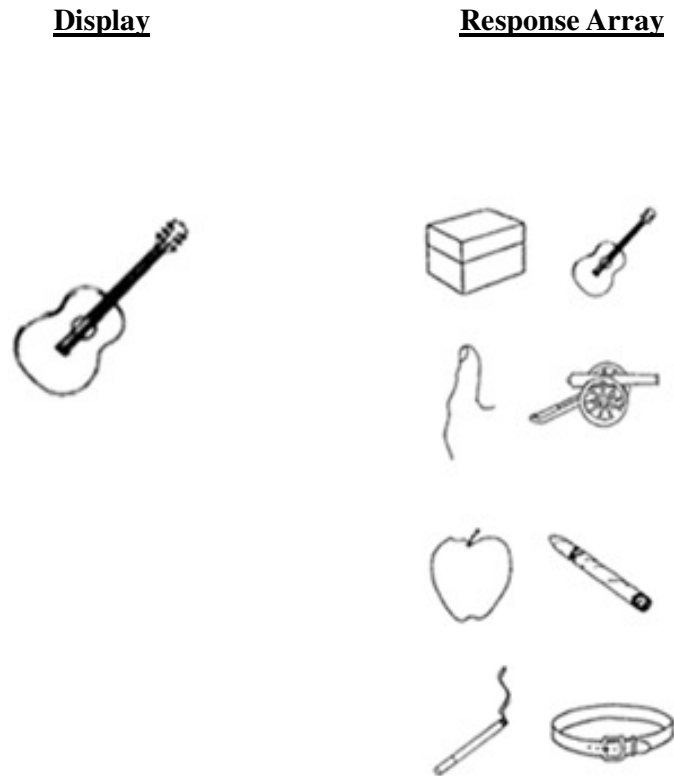


Figure 4 Sample stimulus displays and response sheets (a) Overlapping common object (Task 1), (b) Overlapping abstract shapes (Task 2), and (c) Non-overlapping control (Task 3).

Additionally, the displays were matched for two other factors: familiarity and visual complexity:

Familiarity is defined, according to Snodgrass and Vanderwart (1980) as ‘how usual the object is in your realm of experience’ (ibid. p. 183). Stimulus ratings for familiarity were obtained from the Snodgrass and Vanderwart (1980) norms.

Visual Complexity ratings were obtained from the Snodgrass and Vanderwart (1980) norms according to which complexity is defined by the ‘amount of detail or intricacy of line in the picture’ (ibid. p.183). Complexity is rated on a Likert scale from 1 (very simple) to 5 (very complex).

The mean (SD) familiarity and visual complexity ratings for each cell in the 2 (Semantic relatedness: High/Low) x 2 (Visual Similarity: High/Low) design are shown in Table 2. Using one-way analysis of variance (ANOVA) there was no significant difference in levels of either familiarity; $F(3, 93) = 0.49$; $p = 0.68$; or visual complexity, $F(3, 93) = 1.2$, $p = 0.29$; across cells.

Overlapping figures displays were presented on a single sheet of A4 (210 mm x 297 mm) paper. Accuracy and response time (RTs) were recorded. RTs were timed from the moment that the new trial sheet was presented and stopped when the participant pointed to the last item on the response sheet or indicated that she/he had finished. Trial presentation order was randomized. All participants were instructed to indicate which figures appeared in the overlapping displays, by pointing one-by-one, to the corresponding item on the response sheet.

Table 2.

Mean ratings for Familiarity and Visual Complexity across conditions in Task 1. Standard deviation shown in parentheses.

		Semantic Relatedness			
		High		Low	
		Familiarity	Visual Complexity	Familiarity	Visual Complexity
Visual	High	3.22 (1.02)	3.04 (0.70)	3.49 (0.95)	2.75 (0.91)
	Low	3.42 (0.81)	2.68 (1.07)	3.38 (2.95)	2.95 (0.91)

Task 2: Overlapping Figure Test 2 (Abstract Shapes)

In order to further delineate influences of different stimulus factors on MT's overlapping figures task performance, we developed a version of the test containing overlapping displays of abstract two-dimensional polygons - see Figure 4(b) (Bisiach et al., 1976).

There were nine overlapping display trials each with between 3-5 overlapping figures (N total stimuli = 35). Response displays contained four target and four distracter items.

In order to compare the visual complexity of the common object (Task 1) and abstract shape overlapping displays (Task 2), we conducted a separate rating study. Data were collected from 23 healthy naïve control subjects (mean age 65.5; range 50-75; 11 female). The overlapping displays from both tasks were presented in a random, inter-mixed, order to each control. Visual complexity was assessed using a five point Likert scale (1 = Low; 5 = High) using the definition of visual complexity provided by Snodgrass and

Vanderwart (1980). For the abstract object displays mean complexity was 2.29 (SD = 0.88) compared to 2.87 (SD = 0.76) for the common object displays. These were contrasted using a paired sample t-test by subjects (across mean ratings per item), and an independent samples t-test by items (across mean ratings per subject). The difference was significantly different both by subjects, $t(22) = 2.39$, $p = .026$; and by items, $t(47) = 2.39$, $p = .021$. We discuss the relevance of this difference in the General Discussion.

For Task 2 the testing procedure was identical to Task 1. Response time and accuracy were recorded.

Task 3: Common object non-overlapping control test

This control task was devised to determine whether MT's performance with overlapping figures displays was due to properties of the overlapping displays or because of the requirement to select individual objects from the multi-item response arrays. The stimuli were the same target items shown on the overlapping figure displays in Task 1 (N=32). On each trial, MT was presented with a single target item, and asked to point to the same item on an eight-item response array. Response displays were the same as those used in Task 1 – see Figure 4(c). Accuracy and RT measures were recorded. Onset time commenced on presentation of the first single target item, and stopped immediately following the response to the last target.

Data analysis

Comparisons of RT data between MT and the controls used the modified t-test (Crawford & Garthwaite, 2002; Crawford et al., 2010). Statistical significance was assessed using two-tailed probabilities, and an a priori alpha level of .05. Exact probabilities are stated ($p=x$) except where $p < .0001$.

RESULTS

Analysis of overlapping vs. non-overlapping (control) task performance

Our initial goal was to determine whether MT shows an overall deficit in overlapping figures task performance, and whether any impairment could be specifically related to a deficit in his perceptual analysis of the overlapping figures displays, or rather solely to the response requirements of the task; that is, to the selection of single targets from multiple-item response arrays. Table 3(a) shows the response accuracy across tasks for MT and the controls. As shown, MT performed well within normal limits in terms of his response accuracy on all three tasks.

In contrast, Table 3(b) shows the overall mean RTs (per display item) and z scores for MT and the controls, along with the t-values, and associated statistical significance for each within-task contrast using the modified t-test on the RT data. These analyses show that MT was impaired, relative to controls, in the overlapping common object figures test (Task 1), but he showed no impairment in either the overlapping abstract figures test (Task 2) or in the non-overlapping common object control test (Task 3).

In addition, while MT showed slower mean RTs with overlapping common object (Task 1) displays relative to overlapping abstract displays (Task 2), the controls showed the opposite pattern – they were significantly faster with overlapping common objects than abstract shapes, $t(8) = 11.31, p < .0001$.

Table 3(a).

Accuracy (% correct) for MT and the controls across tasks (collapsed across conditions).
Standard deviation of controls shown in parentheses.

	Mean accuracy (% correct)		
	MT	Controls (SD)	Range
Overlapping Common Object (Task 1)	99.25	99.25 (0.75)	99-100
Overlapping Abstract Shapes (Task 2)	100	97.14 (3.48)	88-100
Non-Overlapping Control (Task 3)	100	100 (0)	-

Table 3(b).

Overall mean RTs (per item), Z scores, modified t , and p statistics for MT and the controls across tasks.
Standard deviation of controls shown in parentheses.

	Mean RT (s)				
	MT	Controls (SD)	Z	t (8)	p
Overlapping Common Objects (Task 1)	5.68	2.12 (0.52)	6.83	8.51	.001
Overlapping Abstract Shapes (Task 2)	3.85	4.11 (0.51)	-0.50	-0.46	ns.
Non-Overlapping Control (Task 3)	2.44	2.42 (0.36)	-0.03	.03	ns.

These data suggest that MT has a deficit in processing overlapping figures displays with common objects (Task 1), but not with abstract shapes (Task 2). In addition, MT's deficit in the overlapping common object task is not due to a difficulty in selecting targets from the multi-item response arrays. In support of this, MT was not impaired in the non-overlapping control task (Task 3), and showed no deficit in either accuracy or RTs in the overlapping abstract shapes task.

Determinants of overlapping figures task performance in MT

Our next goal was to elucidate the factors underlying MT's performance with overlapping common objects. Figure 5 shows the mean RTs for MT and the controls as a function of Semantic Relatedness (High vs. Low) and Visual Similarity (High vs. Low). Separate within-condition contrasts using the modified t-test showed that MT's mean RTs were significantly slower than the controls on both high semantically related; $t(8) = 7.49$, $p < .0001$; and low semantically related displays; $t(8) = 4.83$, $p < .0006$. MT also showed slower RTs than controls on both high visual similarity; $t(8) = 7.21$, $p < .0001$; and low visual similarity displays; $t(8) = 5.44$, $p < .0001$. An inspection of the data pattern in Figure 5 also suggests an interaction between semantic relatedness and visual similarity.

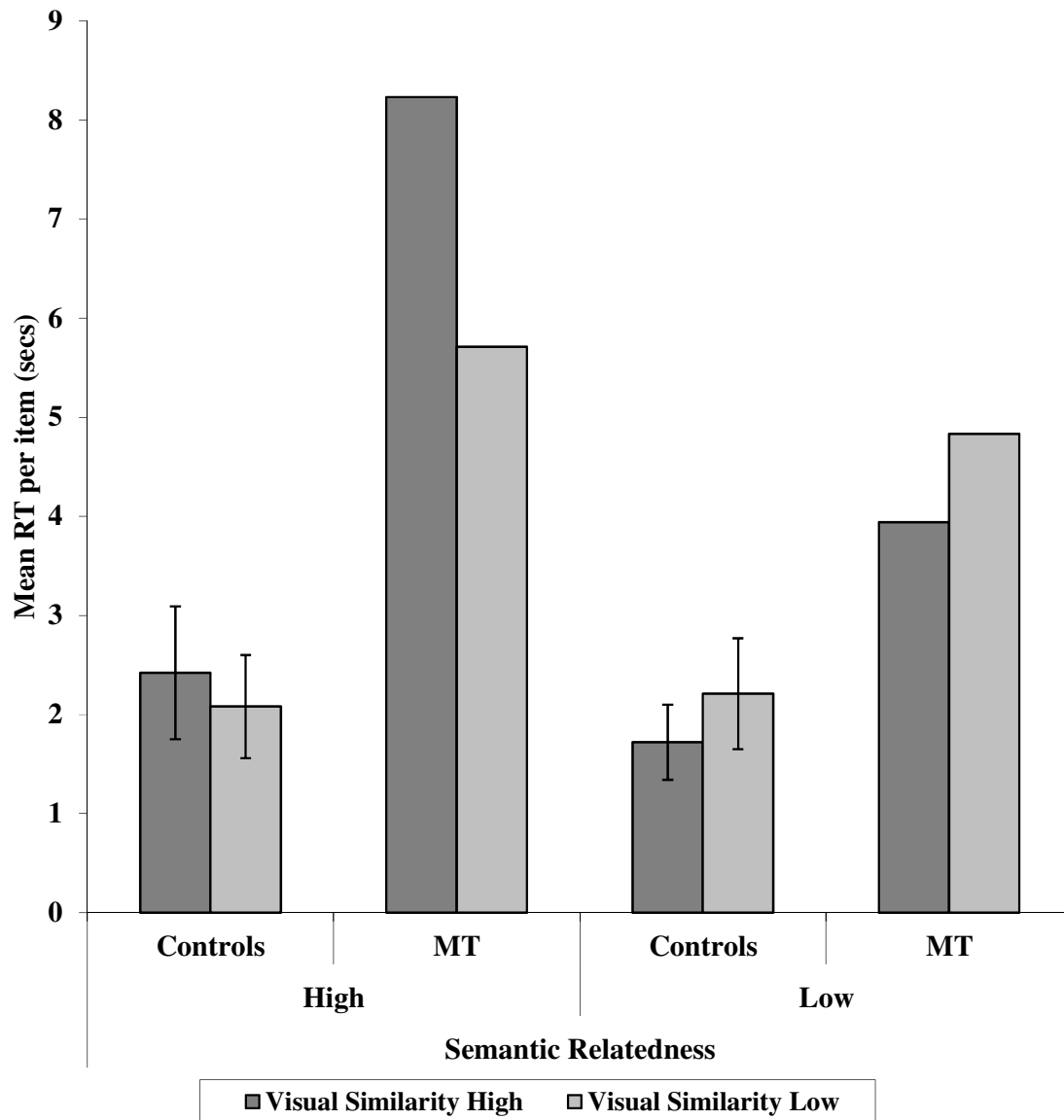


Figure 5 Mean RTs (per item) for the Controls and MT as a function of display type for Task 1 (Common object overlapping displays): Semantic Relatedness (High vs. Low) and Visual Similarity (High vs. Low). Error bars show standard deviation.

We examined this interaction using difference scores (mean per item) computed from the RT data for MT and the controls: Mean RT_{High Semantic Relatedness (High Visual Similarity – Low Visual Similarity)} – Mean RT_{Low Semantic Relatedness (High Visual Similarity – Low Visual Similarity)}. The mean interaction across controls ($M = 0.83s$; $SD = 0.33$) was compared to MT (3.39s) using the modified t-test. This difference was significant, $t(8) = 7.4$, $p < .0001$.

A further analysis was conducted to determine whether the observed interaction could be accounted for solely in terms of average response latency rather than as a consequence of cognitive impairment in MT. If this were case, the control data should show a correlation between interaction size and overall mean RTs. In fact, there was no significant correlation ($r^2 = .30$, d.f. = 1, 7, $p = 0.12$).

GENERAL DISCUSSION

MT sustained ventral posterior lesions encompassing the fusiform gyri (bilaterally), and right calcarine sulcus, V4 and lingual gyrus. On initial examination, MT showed a highly circumscribed pattern of impairment manifest by prosopagnosia, letter-by-letter reading and some difficulties at identifying objects in crowded, overlapping, displays – a clinical profile consistent with ventral simultanagnosia (Farah, 1990). In contrast, he had no difficulty in generating accurate perceptual representations of complex non-overlapping patterns as shown by his performance on the Rey Figure, and MT performed normally on a range of tests assessing low-level vision. MT had no difficulty recognizing line drawings of common objects presented in isolation and was able to match objects across changes in viewpoint.

Despite showing no impairment in single object recognition (in either accuracy or RTs), MT showed a striking pattern of normal and impaired performance in overlapping figures tasks – the focus of the current study. While MT was accurate in his ability to perform overlapping figures tasks with line drawings of common objects his RTs were slower relative to age-matched controls. In contrast, he performed normally (in both accuracy and RTs) with overlapping displays of abstract shapes, and showed no deficit in matching single images of non-overlapping common objects to response arrays containing multiple items.

MT's impaired performance with overlapping common objects relative to displays of abstract shapes cannot be accounted for in terms of visual complexity. Although the abstract shape displays used in Task 2 were rated as significantly less complex than the common objects used in Task 1 (see Methods), controls showed the opposite pattern to MT on the overlapping figures tasks; that is, they were slower to respond to overlapping abstract shapes than to common objects.

Further analyses of MT's performance with overlapping common objects showed that his impairment was modulated by both semantic relatedness and visual similarity, and the effect of these factors interacted: MT's impairment was most pronounced in displays containing items of high semantic relatedness and high visual similarity. These effects also cannot be accounted for by familiarity or visual complexity – as these factors were matched across conditions within the overlapping common object task.

These findings invite speculation about the underlying functional impairment in MT. In the first place, he does not appear to have an obvious deficit affecting the perceptual grouping of local contour elements from bottom-up sensory input: he performs normally in grouping features with overlapping abstract shape displays. Neither does MT appear to have an impairment affecting his ability to select individual objects from multi-item response arrays (as shown by his normal performance in Task 2 with abstract displays, and in the single item control task. We consider two other possibilities.

One hypothesis is that MT's deficit arises from a functional impairment affecting the way in which stored object representations are activated from perceptual input during object recognition. On this account, we might suppose that during recognition the perceptual representation of a given stimulus (e.g., cat) may simultaneously activate the stored representations of several visually and semantically related objects (e.g., cat, dog, sheep). In the normal system, the visual-semantic representations of these competing items may be inhibited allowing preferential processing or selection of a single target. If this were not to occur the system may take longer to achieve recognition which might be the case in MT. However, there is some evidence that MT does not have a deficit affecting the activation patterns of stored object representations *per se*. Indeed, if this were the case then we might expect him to show some impairment in single object recognition – at least in RTs, and this was not the case. Thus, MT is not impaired in accessing or retrieving stored object knowledge¹.

The second hypothesis is that MT's impairment derives from a perceptual deficit

¹ The PACE model (e.g., Gerlach, 2009) specifies two processing stages in recognition: the assembly of a shape representation (binding of shape elements) and selection of a target (shape) representation from among competing objects. This conceptualisation is used to argue for a 'pre-semantic' account of category-specific impairment on the basis of visual similarity (objects from the same amodal semantic category are more likely to share shape configuration). Although our study was not designed to specifically test this issue (and does not speak to category-specificity *per se*) it is perhaps relevant that our evidence supports a role for semantic overlap (independent of shape similarity) as a factor mediating high-level, top-down integration of stored knowledge and sensory input.

affecting the grouping of image features when stored object knowledge is integrated with visual-sensory input. Indeed, the results provide several findings of relevance to theoretical models of shape feature integration during visual perception. In particular, they suggest that feature integration does not wholly precede object recognition in a strictly feedforward manner (e.g., Bar, 2003; Beck & Palmer, 2002; Freeman et al., 2003; Harel, Ullman, Harari & Bentin, 2011; Humphreys et al., 1997; Peterson & Gibson, 1994; Rock, 1962; Twomey et al., 2011). Some broader theoretical context for understanding MT's deficit comes from the recent work of Bar and colleagues (e.g., Bar, 2003; Bar, Kassam, Ghuman et al., 2006; Fenske, Aminoff, Gronau & Bar, 2006). They have argued that on-line perceptual processing during object recognition in the neurologically normal brain is supported by recurrent feedback from the prefrontal cortex (PFC) based on fast, high spatial frequency (HSF), analyses of the perceptual input. Anatomically, this mechanism is hypothesized to be mediated by magnocellular projections from early visual areas V2 and ventral V4 to the ventrolateral PFC (Kveraga, Boshyan & Bar, 2007). As noted above, in patient MT there is no impairment to bottom-up perceptual grouping: he performs normally with overlapping displays of abstract shapes. Neither does he appear to have any difficulty in accessing stored object knowledge or in using this information to constrain object recognition. Within the context of this model of recurrent processing MT's deficit appears to arise at a level of perceptual analysis at which local image features are integrated into coherent

representations of shape and at which this integration is constrained by stored object knowledge. Consistent with other models proposing cascade processes in visual perception (e.g., Freeman et al., 2003; Humphreys et al., 1997), the influence of semantic relatedness and visual similarity on MT's performance suggests that part of the top-down stream contains parallel information about semantic and visually related objects, and that this information is available before feature integration is fully resolved. In the undamaged system, such top-down information may facilitate resolution of ambiguous feature integration outputs; that is, competing perceptual groupings of image contour. In MT, the effects of a deficit affecting how this top-down information is used to constrain perceptual grouping are likely to be magnified in spatially overlapping displays which contain competing perceptual interpretations. And they are likely to be greatest with overlapping displays containing items of high semantic relatedness and high visual similarity – as confirmed by the interaction shown in Figure 5. It is interesting to note also that MT performed significantly more slowly than controls on both displays of high and low visual similarity (collapsing across semantic relatedness), as well as on displays of high and low semantic relatedness (collapsing across visual similarity). This suggests that both can contribute independently to task performance.

A key issue concerns the exact functional deficit in MT that underlies this apparent integration impairment. This is unclear at present. One possibility is that in MT the

processes underlying perceptual grouping have difficulty using prior object knowledge to resolve competing perceptual interpretations of the sensory input (e.g., ‘cat’, ‘dog’, ‘sheep’) – via facilitation of a single target output (e.g., ‘cat’) and/or inhibition of competing outputs (‘dog’, ‘sheep’). As a consequence, it may take longer to select a single target response from among semantically and visually similar objects. So for MT, the activation of prior knowledge effectively adds noise to the system.

Anatomical considerations: V4 and perceptual integration

The focal nature of MT’s brain-damage also invites speculation about the underlying anatomical correlates of his functional deficit. As noted in the case report, MT sustained ventral posterior lesions encompassing the fusiform and lingual gyri, V4 and the right calcarine sulcus. Of these regions, V4 has attracted considerable interest in relation to its putative role in the perceptual integration of complex shape features (e.g., Brincat & Conner, 2004; Cadieu, Kouh, Pasupathy, Connor, Riesenhuber & Poggio, 2007; Pasupathy & Connor, 2001; Schiller, 1993). For example, Pasupathy and Connor (2001), using single cell recording in V4, have shown that specific neurons respond to particular combinations of feature attributes (e.g., right concave curvature). Interestingly, also, V4 has recently been implicated in recurrent, top-down, modulation of neuronal responses during visual word recognition (Twomey et al., 2011) – and, although not the focus of the current study, it is worthwhile noting that MT also shows evidence of letter-by-letter reading, consistent with

a deficit in lexical access. The current findings could be interpreted as support for the hypothesis that V4 is playing a key role in the grouping of complex shape features, and that the derivation of these features is constrained by top-down processing.

Clinical assessment of overlapping figures tasks

Finally, one further aspect of MT's case merits briefly noting: his deficit with overlapping figures displays was only apparent in response time measures. It was not shown in accuracy. Thus, a standard clinical analysis of performance accuracy would not be sufficient to uncover his perceptual deficit (e.g., Bisiach et al., 1976; De Renzi et al., 1969; Della Salla et al., 1995). In addition, the use of the overlapping figures task in clinical evaluations should also be sensitive to the potential influence of both perceptual and top-down knowledge in affecting task performance.

Conclusion

In summary, MT's performance in the overlapping figures task was modulated by the semantic relatedness and visual similarity of display items, as well as by object familiarity: he was not impaired with overlapping displays of abstract shapes. In contrast, he showed no evidence of impairment in object recognition when presented with single stimuli, or in selecting items from multi-item response arrays. These findings challenge claims that visual perception is driven solely by feedforward mechanisms, and show how brain-damage can selectively impair high-level perceptual processes supporting the

integration of stored knowledge and visual sensory input. We propose that MT's difficulties reflect the impairment to a level of perceptual analysis mediated by V4 at which stored visual-semantic object knowledge constrains the perceptual integration of sensory information during the perception of shape.

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