Noun and knowledge retrieval for biological and non-biological entities following right occipitotemporal lesions

Rose Bruffaerts[1,2], An-Sofie De Weer[1], Sophie De Grauwe[1,3], Miek Thys[1], Eva Dries[1], Vincent Thijs[2], Stefan Sunaert[4],Mathieu Vandenbulcke[5,6], Simon De Deyne[7], Gerrit Storms[7], Rik Vandenberghe[1,2]

[1]Laboratory for Cognitive Neurology, Department of Neurosciences, KU Leuven, Belgium, [2]Neurology Department, University Hospitals Leuven, Leuven, Belgium, [3]Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Nijmegen, The Netherlands, [4]Radiology Department, University Hospitals Leuven, Leuven, Belgium, [5]Brain and Emotion Laboratory Leuven, Department of Neurosciences, KU Leuven, Belgium, [6]Psychiatry Department, University Hospitals Leuven, Leuven, Belgium, [7]Laboratory of Experimental Psychology, University of Leuven, Leuven, Belgium

Corresponding author: Rik Vandenberghe, M.D., Ph.D., Neurology Department, University Hospitals Leuven, Herestraat 49, 3000 Leuven, Belgium, e-mail: rik.vandenberghe@uz.kuleuven.ac.be, phone: ++ 32 (0)16 344280, fax: ++ 32 (0)16 344285

Abstract

We investigated the critical contribution of right ventral occipitotemporal cortex to knowledge of visual and functional-associative attributes of biological and non-biological entities and how this relates to category-specificity during confrontation naming. In a consecutive series of 7 patients with lesions confined to right ventral occipitotemporal cortex, we conducted an extensive assessment of oral generation of visual-sensory and functional-associative features in response to the names of biological and nonbiological entities. Subjects also performed a confrontation naming task for these categories. Our main novel finding related to a unique case with a small lesion confined to right medial fusiform gyrus who showed disproportionate naming impairment for nonbiological versus biological entities, specifically for tools. Generation of visual and functional-associative feature was preserved for biological and non-biological entities. In two other cases, who had a relatively small posterior lesion restricted to primary visual and posterior fusiform cortex, respectively, retrieval of visual attributes was disproportionately impaired compared to functional-associative attributes, in particular for biological entities. However, these cases did not show a category-specific naming deficit. Two final cases with the largest lesions showed a classical dissociation between biological versus nonbiological entities during naming, with normal feature generation performance. This is the first lesion-based evidence of a critical contribution of the right medial fusiform cortex to tool naming. Second, dissociations along the dimension of attribute type during feature generation do not co-occur with category-specificity during naming in the current patient sample.

1. Introduction

How the right hemisphere contributes to the processing of identity and knowledge of concrete entities, is an important topic within cognitive neuroscience. A key source of evidence have been lesions in humans and how they affect lexical and semantic retrieval for different semantic categories, attributes and input-modalities.

Category-specific deficits for biological entities are most often reported following bilateral or left-sided (Forde et al., 1997; Sartori and Job, 1988; Warrington and Shallice, 1984; Gainotti, 2000; Capitani et al., 2003) rather than right-hemispheric lesions (Vandenbulcke et al., 2006; Capitani et al., 2009). In a case series of posterior cerebral artery (PCA) stroke patients who were tested for category-specific deficits (Capitani et al., 2009), half of the 8 subjects with a right-sided lesion had impaired naming. Given the impairment on the object decision task in these patients and the between-task inconsistency, the naming deficit could have partly originated from visuoperceptual rather than semantic dysfunction (Capitani et al., 2009). Most other reports on semantic impairment following a lesion to the right hemisphere are based on single cases. BD (Hankey et al., 1989) showed impaired identification of people and other biological entities, while nonbiological entities (including musical instruments) were spared. Case SM, who suffered a complete right PCA infarction (Turnbull and Laws, 2000), was impaired on low-familiarity artifacts versus low-familiarity biological entities.

Deficits in retrieving knowledge about concrete entities following focal right occipitotemporal lesions have also been described. JA (Vandenbulcke et al., 2006), who suffered a stroke in right mid-posterior fusiform gyrus, was impaired on tasks probing explicit retrieval of visual-sensory compared to functional-associative features through both verbal (feature generation, forced-choice naming to definition) and nonverbal means (drawing from memory). Despite a selective impairment of retrieval of visual features, JA did not demonstrate a semantic category effect, biological versus non-biological (Vandenbulcke et al., 2006). A large number of reports have confirmed that a deficit for specific attribute types (e.g. visual-sensory attributes) and a deficit for specific categories (e.g. biological entities) are not necessarily coupled (Laiacona et al., 1993, 1997; Moss et al., 1998; Lambon Ralph et al., 1998; Capitani et al., 2009; Mahon et al., 2009; Mahon and Caramazza, 2011). This has important theoretical implications as theories such as the sensory-functional theory (Warrington and Shallice, 1984; Flores d'Arcais et al., 1985; Farah et al., 1991) would lead one to predict such a coupling.

By conducting a systematic consecutive study in right ventral occipitotemporal lesion patients, we wanted to gain insight into the relationship between knowledge for specific attribute types and knowledge for specific categories. We used a naming task that had been specifically designed to test category-specific naming deficits while controlling for stimulus familiarity and visual complexity (Laiacona et al., 1993). Within the same subjects, we studied generation of attributes of biological and nonbiological entities so that we could relate any category effects to deficits organized according to attribute type (Vandenbulcke et al., 2006). In order to detect changes in visuoperceptual identification sensitively, subjects also performed a speeded word and picture identification task (Vandenbulcke et al., 2007). Through the combination of these 3 tasks we determined the prevalence of category-specific defects following right ventral occipitotemporal lesions as well as the relationship with deficits in retrieving specific attribute types and in visuoperceptual identification.

2. Methods

2.1. Participants

Patients with lesions restricted to the right occipitotemporal cortex on clinical fluid attenuated inversion recovery (FLAIR) or diffusion-weighted MRI were consecutively recruited via the acute stroke unit of the University Hospitals Leuven, Belgium, or on the occasion of a visit to the outpatient memory or stroke clinic (Table 1, Figure 1). The lesions were due to ischemic stroke (cases 2, 3, 5-7), cerebral venous thrombosis (case 4) or to traumatic brain injury (case 1). Exclusion criteria were age above 80 years, pre-existing structural lesions or extensive periventricular or subcortical white matter hyperintensities on MRI and insufficient balance to sit autonomously in front of a computer. We screened a consecutive series of 1225 patients, 7 of whom fulfilled the inclusion criteria (Table 1). The main reasons for exclusion were age, presence of pre-existing brain lesions and inability to sit in a chair and fully cooperate for the duration of the experiment because of neurological or medical reasons. Each of the participants received a detailed clinical-neurological history and examination by a clinical neurologist at the time of testing. Apart from visual quadrantanopia this did not reveal any abnormality.

Control subjects were 23 community-recruited age-matched volunteers (11 men, mean age: 60.3 years old, S.D. 3.4 years) without neurological or psychiatric history. The study was approved by the Ethics Committee, University Hospitals Leuven. All participants provided written informed consent in accordance with the Declaration of Helsinki.

Case	**Age**	**Sex**	**Oldfield**	**Time**	**Volume(cm^3)**	**Pathology**
2	68	M	1	1.5 m	47.61	ischemic stroke
1	57	F	0.5	8.5 yr	25.79	traumatic brain injury
3	53	M	1	4 m	18.81	ischemic stroke
6	31	F	1	6.7 m	18.53	ischemic stroke
4	52	F	1	1 m	2.72	cerebral venous thrombosis
7	52	M	0.8	4 m	1.65	ischemic stroke
5	57	M	-0.6	4 m	0.69	ischemic stroke

Table 1 – Patient characteristics: Abbreviations: M = male, F = female, handedness based on Oldfield (1971), time = time-to-lesion onset, O = Occipital cortex, T = temporal cortex, OT = occipitotemporal cortex. Case numbers indicate the order of recruitment, cases are ordered according to decreasing lesion volume.

2.2. Experimental tests

Stimulus presentation and response registration were controlled by a PC running Presentation 11.3 (Neurobehavioral systems, Albany, CA). Participants were seated at 60 cm from a 19-inch cathode ray tube monitor (resolution: 1024 x 768 pixels, refresh rate: 75 Hz).

Prior to the experimental tests, visual acuity was tested binocularly by means of a Snellen chart on the computer screen in front of the subject. A digitized visual field perimetry was also performed (Molenberghs et al., 2008): A grey circular patch (duration: 500 ms) was presented at 16 different locations: The stimulus was presented at either 2° (stimulus size 0.8°) or 5° eccentricity (stimulus size 2°) on the vertical or horizontal meridian or on the diagonals. Each location was tested a total of five times. The order between locations was randomized as well as the interstimulus interval (random variation within a range of 500-4000 ms). Subjects were instructed to respond by button press to the appearance of the stimulus while fixating a central 0.48° black square.

2.2.1. Speeded word and picture identification

The purpose of this task was to detect changes in visuoperceptual identification of words or pictures in a sensitive manner by presenting stimuli from very short to longer durations (Bundesen, 1990; Vandenbulcke et al., 2007). Subjects had to read names of 69 biological entities and 91 nonbiological entities or name pictures (Snodgrass and Vanderwart, 1980) of these entities. Word or picture duration varied between 30, 60, 90, 150, 200, 500, 800 or 2000 ms. A trial consisted of a warning sound, a forward mask (200 ms duration, 9.68° x 7.74°), followed by a picture (9.68° x 7.74°) or word (letter height: 1°), which was immediately followed by a backward mask (200 ms duration, 9.68° x 7.74°) and a fixation point for 3 seconds. Per subject each stimulus was shown once as a word and once as a picture. Within a same run a same stimulus was never shown in both modalities. Each subject underwent a total of 4 runs, each containing 40 words and 40 pictures. Within each run, there were 5 words and 5 pictures for each of the 8 possible stimulus durations. A picture name was considered correct when it corresponded to the target word or a synonym of the target word or when it had occurred in at least 3 out of 30 healthy controls viewing the picture for 2 s in an independent cohort. If in doubt, subjects were encouraged to guess.

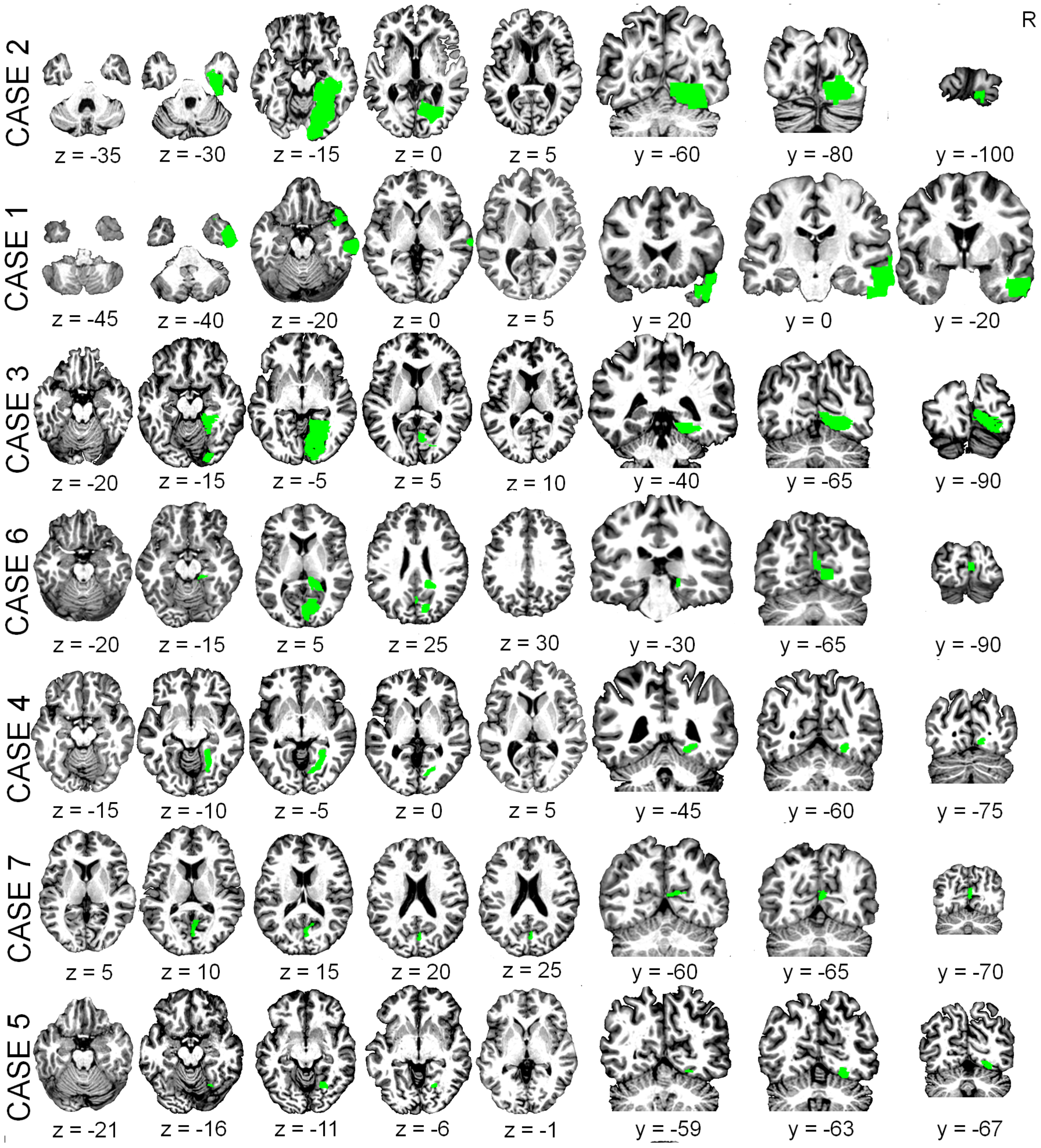

Figure 1 – Lesion distribution: Lesion maps of cases 1-7 (green) projected on T1-weighted images with MRIcron (Rorden et al., 2007). Coordinates are in M.N.I.

For each individual, the onset, slope, and asymptote of the time-accuracy function for words and pictures were calculated by means of the equation: accuracy = $c*(1-e^{(a-\Delta t)/b})$ for $\Delta t \geq a$ (Verhaeghen et al., 1998). Δt stands for presentation time, a is the onset time when the curve starts to rise, b the slope of the curve (the 'rate of approach') (Bundesen, 1990), and parameter c corresponds to the asymptote (Verhaeghen et al., 1998). Higher values of b indicate that the time-accuracy function is less steep, that is, participants with higher b values need more processing time in order to reach the asymptotic level of performance than participants with lower values. Goodness of fit was estimated as the sum of squared differences between the measured and calculated values (sum of the squared errors), as calculated by means of the Optimization Toolbox for Matlab (Mathworks, Natick, MA, USA). We compared each of the parameters for words and pictures with that of the control group by means of a modified t-test (Crawford and Garthwaite (2005); statistical threshold one-tailed P of 0.05).

In order to further explore any laterality bias in processing the stimuli, we examined word identification errors and searched for any lateralization in the letters omitted at presentation durations of 90 ms or higher.

2.2.2. Confrontation naming

The purpose of the confrontation naming task was to detect category-specific deficits during naming. In the confrontation naming task (Laiacona et al., 1993; Laiacona and Capitani, 2001; Vandenbulcke et al., 2006), subjects had to name 60 line drawings from the Snodgrass-Vanderwart set (Snodgrass and Vanderwart, 1980), covering three biological categories (10 animate, 10 fruits and 10 vegetables) and three nonbiological categories (10 tools, 10 items of furniture and 10 vehicles). Categories were matched for frequency, visual complexity, familiarity, image agreement and prototypicality (Snodgrass and Vanderwart, 1980). The stimuli were presented foveally at a visual angle of 9.68° x 7.74°. A warning sound (10 ms) preceded the presentation of each stimulus by 500 ms. The maximum duration of stimulus presentation was limited to 60 s. Once the subject had responded, the examiner started the presentation of the next trial. Responses were considered correct if they were the picture's dominant name, a synonym, the name of a subordinate to the entity designated by the dominant name, or else if it occurred in at least 3 out of 30 other healthy controls viewing the picture for 2 s. Spontaneous, immediate auto-corrections were allowed.

Voice onset times were measured for correct responses based on the onset of the warning sound and the onset of the first phoneme of the correct noun pronounced, using WavePad Sound Editor Masters Edition v 5.05 (NCH Software, Canberra, Australia). Voice onset times were calculated to the onset of the picture.

We compared the individual patients' accuracies and voice reaction times on biological and nonbiological items with that of the control group by means of a modified t test (Crawford and Garthwaite (2005); statistical threshold one-tailed P of 0.05). For a 'classical dissociation' (Crawford et al., 2003), the patient had to be significantly impaired on either biological or nonbiological entities compared to control subjects (not on both), and the discrepancy between the two categories had to be statistically different from the discrepancy observed in control subjects (revised standardized difference test; Crawford and Garthwaite (2005); two-tailed P of 0.05). A strong dissociation was considered to be present if both categories were impaired, but to a different degree (Shallice, 1988). The class of 'biological entities' encompasses living entities, fruits and vegetables.

2.2.3. Feature generation

The purpose of the feature generation task was to evaluate whether patients who exhibit a dissociation between biological and nonbiological entities during confrontation naming, also exhibit a disproportionate impairment in the generation of visual versus functional-associative features.

The entities used were based on normative data collected by Ruts et al. (2004) and covered a range of frequencies and typicalities (Ruts et al., 2004). Feature generation data were obtained in more than 1000 students for these entities from which a concept-feature matrix can be derived (De Deyne et al., 2008; De Deyne and Storms, 2008a,b; Bruffaerts et al., 2013). Based on this concept-feature matrix we performed multidimensional scaling and hierarchical clustering for the largest group (living animals) in order to derive semantic clusters. These clusters are indicated by dotted lines in Fig. 3.

In the feature generation task a written name of a concrete entity was presented foveally (letter height: 1°) on the screen for 1 minute. Subjects were instructed to recite as many different kinds of characteristics as possible within that minute, e.g. what the entity looked like, what it was used for, where it came from, etc. The relatively long interval between the items allows the subject to exhaustively report all knowledge that they possess on an entity and avoids a bias towards the most distinctive features. We probed on average 5 entities per category and 11 different categories (8 biological, 3 nonbiological). Eleven of the entities tested in the feature generation overlapped with the entities used in the confrontation naming. Responses were recorded and archived and analysed off-line.

The first step of the analysis consisted of the classification of each of the features generated per entity. This classification was based on the structure proposed by Cree and McRae (2003). We assigned each of the features to one of three attribute types: visual attributes, nonvisual sensory attributes, and, thirdly, functional-associative attributes (Vandenbulcke et al., 2006). The designation 'functional-associative' is used here more broadly than an entity's function as such and includes not only functional but also encyclopedic and taxonomic features, as well as features referring to the manipulation of artefacts. Subjective comments made by the participants (e.g. "I am fond of this item.") were excluded from further analysis.

For each individual and each entity we determined the absolute number of visual attributes generated. Next we averaged these values over all biological entities for each subject and, separately, over all nonbiological entities. We compared the values obtained for each patient with the control group by means of a modified *t* test (Crawford and Garthwaite, 2005) (statistical threshold one-tailed P of 0.05). We also tested for dissociations between the two categories (revised standardized difference test; Crawford and Garthwaite (2005); two-tailed P of 0.05).

For each individual and each entity we also determined the relative number of visual attributes by dividing the absolute number of visual features by the total number of features generated by this subject for that entity. This was expressed as a percentage. This normalization controls for overall differences in fluency between subjects. We compared the values obtained for each patient with the control group based on Crawford and Garthwaite (2005) (statistical threshold one-tailed P of 0.05). We also tested for dissociations between the two categories (Crawford and Garthwaite, 2005).

Third, for each individual we calculated in how many entities the relative number of visual attributes was below 1 S.D. of the control group. We determined a normal number by a comparison of each control subject with the norms based on the other 22 control subjects. Next we compared the number obtained in each patient case with the 23 control subjects by means of a modified t-test (Crawford and Garthwaite (2005); statistical threshold one-tailed P of 0.05).

2.3. Within-item consistency between confrontation naming and feature generation

In those cases who showed a significant impairment on the naming or the feature generation task, we examined for the items that were affected and were present in both tasks whether the deficit generalized across the two tasks.

2.4. Structural MRI

Structural images were acquired on a 3 T Philips Intera system (Best, The Netherlands) equipped with an 8-channel head volume coil. Structural imaging sequences consisted of a T1-weighted 3D turbo-field-echo sequence (repetition time (TR) = 9.6 ms, echo time (TE) = 4.6 ms, in-plane resolution = 0.97 mm, slice thickness = 1.2 mm) and FLAIR (TR = 11000 ms, TE = 150 ms, in-plane resolution = 0.45 mm, slice thickness = 4 mm). Using Statistical Parametric Mapping 2008 (SPM8) (Welcome Trust Centre for Neuroimaging, London, UK), we co-registered the T1 and FLAIR images of each patient. The boundary of the lesion was delineated manually on the individual MR images in subject space for every transverse slice (voxel-resolution 1 x 1 x 1 mm^3) with MRIcron (Rorden et al., 2007). This resulted in a lesion mask. The T1-weighted image was segmented and the resulting parameters were used to spatially normalize each image as well as the lesion mask into standard MNI space.

3. Results

3.1. Visual acuity and digitized perimetry

On the Snellen test, visual acuity was at least 20/50 (able to identify letters with a height of 0.59°) in all patients. Cases 2, 3 and 6 displayed a left upper quadrantanopia for the stimuli presented at 5°, perceiving the stimulus in less than half of the trials. In case 2, the left upper quadrantanopia extended into the central visual field (stimuli presented at 2°). Case 7 suffered a lesion to the right primary visual cortex and presented with left hemianopia, but at the time of testing this deficit was no longer found.

3.2. Speeded word and picture identification

Cases 1-3 showed a reduction in slope for both words and pictures (Table 2; Figure 2). In cases 6 and 7 the slope was significantly reduced for words but not for pictures (Figure 2).

For the word condition, we evaluated whether any lateralized bias was present during speeded identification (Table 3). In cases 2, 3, 6 and 7, errors at short stimulus duration mainly consisted of substitution of the initial, left-sided letters, with preservation of the final, right-sided letters. In these cases, processing of the contralesional field may be disadvantaged, either due to visuoperceptual defects or an attentional bias. Case 1 exhibited the opposite pattern, with preservation of the initial letters.

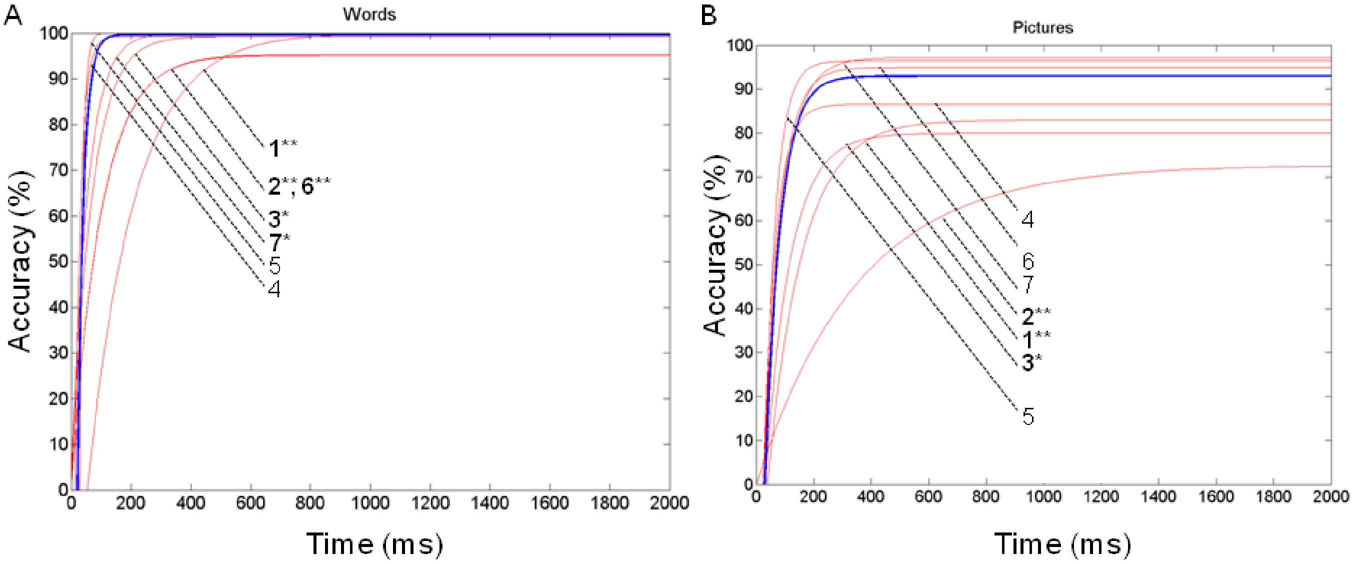

Figure 2 – **Speeded identification:** Speeded identification task for (A) words and (B) pictures. Time-accuracy curves are depicted for controls (averaged over 23 controls, blue) and patient cases (red). Curves with a pathological slope (Table 2) are marked (* P<0.05 ** P<0.001).

		Words			**Pictures**	
	onset	slope	asymptote	onset	slope	asymptote
Controls: Mean	20.52	20.52	99.70	31.55	52.74	92.96
S.D.	6.76	10.08	0.52	13.38	17.12	5.10
Case 2	0	**97.51**	**95.15**	*0*	**353.13**	**72.70**
Case 1	**53.61**	**155.92**	100	39.16	**120.22**	*82.98*
Case 3	0	*66.24*	99.26	31.27	*85.28*	*79.96*
Case 6	0	**98.55**	**95.32**	27.16	53.71	94.93
Case 4	12.26	19.21	99.31	24.60	42.01	86.54
Case 7	0	*51.71*	100	24.03	63.29	97.12
Case 5	28.28	10.56	100	28.82	38.45	96.40

Table 2 – Speeded identification task: Onset (a), slope (b) and asymptote (c) parameters for words and pictures. P-values of the parameters were calculated by means of a modified t test (Crawford and Garthwaite, 2005). Bold: P<0.001. Italic: P<0.05.

Case	Written word	Duration (ms)	Response
Case 2	ster	200	speer
	bureel	200	steel
	kers	200	rups
	pinda	200	panda
	pen	150	been
Case 1	koffer	500	ko
	selder	200	sel
Case 3	kruk	150	bril
	gitaar	150	gevaar
	haar	90	schaar
Case 6	hoed	2000	goed
	uil	500	ui
	haan	200	baan
	pijp	200	kuip
	sigaar	150	gevaar
	kroon	150	kanon
	kruk	150	kruik
	harp	90	trap
	slak	90	ak
	ring	90	tang
	schaar	90	aar
	jurk	90	ark
	viool	90	stoel
	taart	90	hart
Case 7	bobijn	150	robijn

Table 3 – Speeded word identification errors: The target-error pairs are listed for every case with errors at durations of at least 90 ms.

3.3. Confrontation naming

The control group named 28.6/30 biological entities correctly (S.D. 1.31) and 29.2/30 nonbiological entities (S.D. 0.93). Mean voice onset reaction times were 1549 ms (S.D. 404) and 1412 ms (S.D. 362), respectively.

Among the right occipitotemporal lesion patients, we found dissociations between biological and nonbiological entities in both directions. Cases 1 and 2 displayed a significant naming impairment for biological entities and a classical dissociation between biological and nonbiological entities (Table 4). The naming errors consisted of omissions, generalizations as well as visuoperceptual misidentifications (Table 5). In case 2, voice onset times to correctly identified biological items were also significantly slower than in controls, with a significant dissociation between biological and nonbiological entities (Table 4B).

Inversely, case 4 showed a significant naming impairment for nonbiological entities compared to controls and a classical dissociation between nonbiological and biological entities (Table 4). In case 4, the majority of errors pertained to tools, which the patient named as another tool or for which the patient used a neologism containing an action term (Table 5). The classical dissociation was confirmed when we restricted the normal control group to women: compared to female controls, case 4 had a category-specific naming deficit for non-biological entities ($P = 0.009$), with a classical dissociation between biological and non-biological entities ($P = 0.007$). Case 4 named significantly less tools correctly than the 12 women from the control group (case 4: 7/10, mean: 9.4, S.D. 0.79, P = 0.007). Voice onset times for correct responses to tools were within the normal range (1915 ms, mean female controls 1597 ms, S.D. 427, $P = 0.246$).

Case 3 was impaired on the confrontation naming of both categories (Table 4).

	Biological entities		**Nonbiological entities**		**Dissociation**
			Accuracy (/30)		
Controls: Mean	28.6		29.2		
S.D.	1.31		0.93		
		P		*P*	*P*
Case 2	**19**	**<0.001**	29	0.429	**<0.001**
Case 1	**25**	**0.006**	30	0.198	**0.006**
Case 3	**26**	**0.032**	**26**	**0.002**	0.260
Case 6	30	0.154	29	0.429	0.309
Case 4	30	0.154	**26**	**0.002**	**0.001**
Case 7	30	0.154	30	0.198	0.882
Case 5	30	0.154	30	0.198	0.882
			Voice onset reaction times (ms)		
Controls: Mean	1549		1412		
S.D.	404		(S.D. 362)		
		P		*P*	*P*
Case 2	**4607**	**<0.001**	2028	0.056	**<0.001**
Case 1	2026	0.132	1794	0.157	0.916
Case 3	1429	0.387	913	0.097	0.350
Case 6	1580	0.470	1438	0.471	0.999
Case 4	935	0.077	960	0.118	0.811
Case 7	1893	0.208	1031	0.159	0.108
Case 5	1390	0.352	1525	0.382	0.538

Table 4 – Confrontation naming: Accuracies and voice onset reaction times for biological and nonbiological items. P-values were calculated by means of a modified t-test (Crawford and Garthwaite, 2005). To evaluate dissociation between biological and nonbiological items, a two-tailed revised standardized difference test was used (Crawford and Garthwaite, 2005).

Case	Entity	Reponse	Entity (English)	Response (English)
Case 2	Selder	Groente	Celery	Vegetable
	Artisjok	-	Artichoke	-
	Asperge	-	Asparagus	-
	Maïs	-	Mais	-
	Paprika	-	Pepper	-
	Ui	-	Onion	-
	Sla	-	Lettuce	-
	Druif	-	Grape	-
	Meloen (schijf)	-	Mellon (slice)	-
	Sinaasappel	Bol	Orange	Sphere
	Struisvogel	Vogel	Ostrich	Bird
	Schommelstoel	Stoel	Rocking chair	Chair
Case 1	Rups	-	Caterpillar	-
	Zwaan	Gans	Swan	Goose
	Struisvogel	Vogel	Ostrich	Bird
	Artisjok	-	Artichoke	-
	Meloen (schijf)	Boot	Mellon (slice)	Boat
Case 4	Moersleutel	"Draaischroef"	Wrench	"Turning Screw"
	Tang	Schroevendraaier	Pliers	Screwdriver
	Bijl	Hamer	Axe	Hammer
	Schommelstoel	"Wiegstoel"	Rocking chair	"Cradling chair"

Table 5 – Confrontation naming errors in cases with a significant dissociation: The target-error pairs are listed for every case with significant dissociation. Omissions are indicated by "-". Quotation marks indicate neologisms.

3.4. Feature generation

In absolute numbers, for biological entities, the control group produced on average 2.691 (S.D. 0.819) visual attributes, 0.242 (S.D. 0.107) sensory nonvisual attributes and 6.074 (S.D. 1.580) functional-associative attributes per entity. For nonbiological entities, controls produced on average 2.417 (S.D. 0.868) visual attributes per entity, 0.242 (S.D. 0.175) sensory nonvisual attributes and 6.011 (S.D. 1.571) functional-assiociative attributes (Table 6A). No significant differences were found in the absolute number of visual attributes generated by men versus women for biological (Wilcoxon rank sum test: $P = 0.207$) or nonbiological entities (Wilcoxon rank sum test: $P = 0.389$).

None of the patients exhibited a significant decrease in absolute number of visual attributes generated (Table 6A). None of the patients showed a significant deficit for sensory nonvisual or functional-associative attributes.

Proportionally, case 5 and 7 produced relatively fewer visual attributes than controls but only for biological entities (Table 6C). Furthermore, in both cases the number of biological entities for which the proportion of visual attributes generated was below the lower limit of the normal range was pathologically increased (Figure 3, Table 6D). These two cases had the smallest lesions within our group (Table 1). Case 7 had a lesion restricted to the primary visual cortex and parieto-occipital sulcus (Figure 1). In case 5 the lesion was limited to the right posterior fusiform gyrus (Figure 1).

Across the 3 different outcome parameters, case 7 showed a systematic dissociation between biological and nonbiological entities, with biological entities being more impaired (Table 6A, C-D; Fig. 3). Case 5 showed a similar dissociation but only for one of the parameters (number of items with a decrease in the relative proportion of visual attributes) (Table 6D).

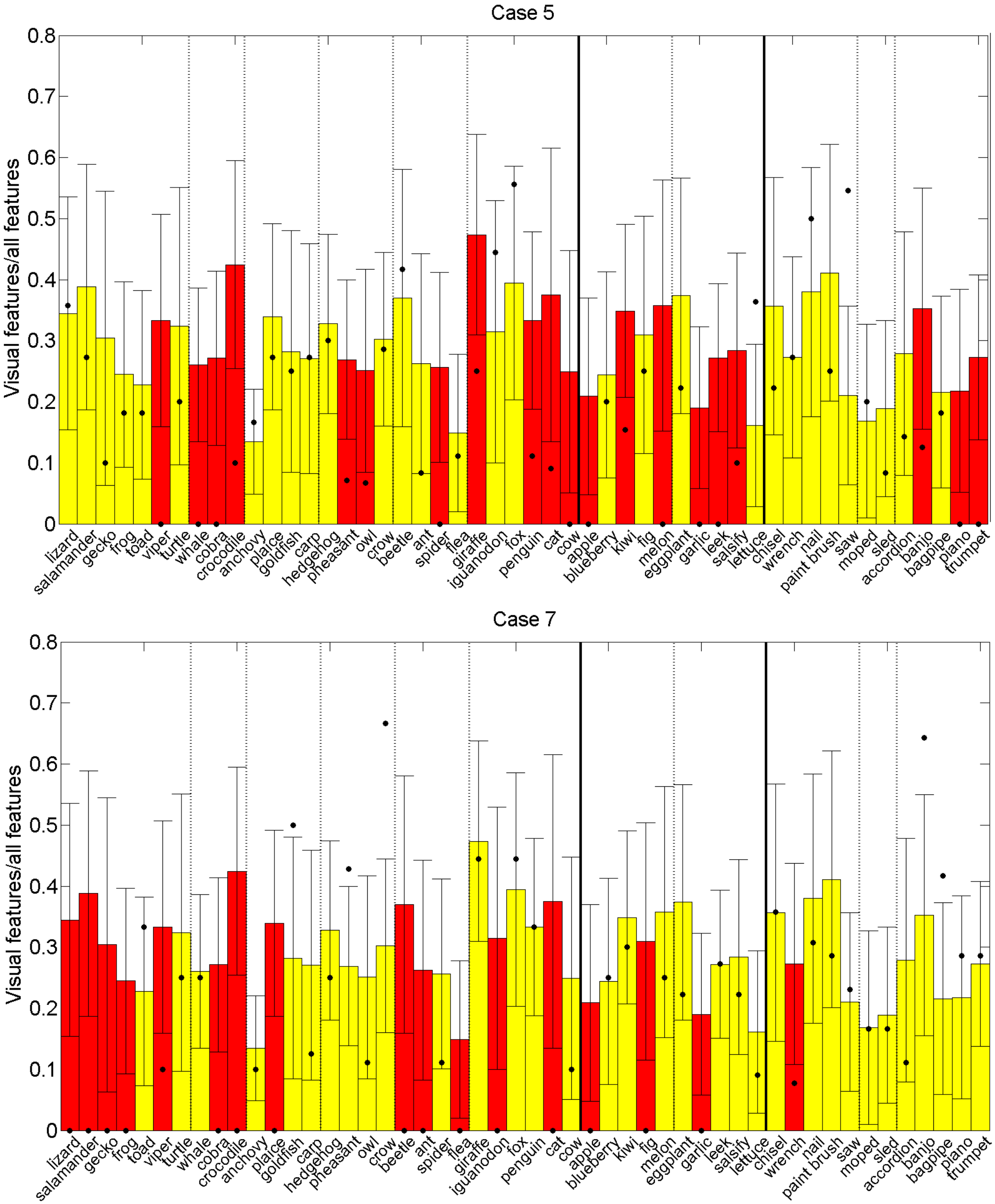

Figure 3 – Feature generation histograms per entity: For all entities (X axis), the Y axis indicates the proportion of the visual feature type generated by 23 control subjects (bar: mean, whiskers: 1 S.D), as well as the proportion for cases 5 and 7 (dot). Red bars indicates that the proportion of the visual feature type for an entity is at least 1 s.d below the mean for this patient. Animate entities were ordered according to the results of multidimensional scaling and hierarchical clustering (vertical dotted lines) derived from the concept feature matrix of De Deyne et al. (2008).

	Biological entities		**Nonbiological entities**		**Dissociation**
A. Mean absolute number of visual attributes					
Controls	2.691 (S.D. 0.819)		2.417 (S.D. 0.868)		
		P		*P*	*P*
case 2	2.086	0.233	1.833	0.259	0.714
case 1	2.028	0.213	1.917	0.289	0.932
case 3	4.278	0.033	3.333	0.156	0.164
case 6	3.000	0.355	2.583	0.426	0.757
case 4	3.868	0.082	3.417	0.136	0.645
case 7	1.342	0.057	3.500	0.117	**<0.002**
case 5	1.842	0.155	2.250	0.426	0.189
B. Mean absolute number of functional-associative attributes					
Controls	6.074 (S.D. 1.580)		6.011 (S.D. 1.571)		
		P		*P*	*P*
case 2	4.029	0.104	4.333	0.154	0.719
case 1	5.278	0.309	5.333	0.338	0.372
case 3	6.889	0.305	6.750	0.325	0.942
case 6	5.389	0.334	4.917	0.251	0.676
case 4	6.974	0.287	7.000	0.272	0.924
case 7	7.210	0.240	8.250	0.088	0.267
case 5	8.711	0.055	7.417	0.195	0.225
C. Mean relative number of visual attributes (%)					
Controls	29.5 (S.D. 6.7)		27.7 (S.D. 7.5)		
		P		*P*	*P*
case 2	31.4	0.394	30.0	0.383	0.866
case 1	26.3	0.325	26.5	0.441	0.500
case 3	36.5	0.160	33.7	0.223	0.769
case 6	31.8	0.373	27.7	0.498	0.643
case 4	33.8	0.270	30.3	0.371	0.703
case 7	**16.2**	**0.032**	27.8	0.496	**0.002**
case 5	**16.9**	**0.039**	20.7	0.197	0.078
D. Number of entities with a decrease in proportion of visual attributes					
Controls	6.522 (S.D. 4.209)		2.522 (S.D. 2.086)		
		P		*P*	*P*
case 2	6	0.363	2	0.404	0.866
case 1	5	0.452	1	0.241	0.367
case 3	1	0.106	2	0.404	0.120
case 6	7	0.456	2	0.404	0.585
case 4	1	0.106	0	0.125	0.874
case 7	**16**	**0.019**	1	0.241	**<0.001**
case 5	**17**	**0.012**	3	0.412	**0.002**

Table 6 – Feature generation: A. Absolute values and P-values for the visual feature type of biological and nonbiological items. **B.** Absolute values and P-values for the functional-associative feature type of biological and nonbiological items. **C.** Mean values: percentage of attributes generated that belonged to the visual type. **D.** Number of entities with a low proportion of visual attributes (<1 S.D. of norms) and P-values for biological and nonbiological items. P-values were calculated by means of a modified one-tailed t-test Crawford and Garthwaite (2005). To evaluate dissociation between biological and nonbiological items, a two-tailed revised standardized difference test was used (Crawford and Garthwaite, 2005).

3.5. Consistency between confrontation naming and feature generation

Given the tool naming deficit seen in case 4 in the confrontation naming task, we conducted an exploratory analysis where we divided the functional-associative features generated by case 4 for the 12 inanimate entities into manipulative actions accomplished with the objects and notions about the object's function (Buxbaum et al., 2000; Buxbaum and Saffran, 2002; Boronat et al., 2005). The number of features referring to object manipulation ($P = 0.359$) or to object function ($P = 0.263$) in case 4 did not differ from the values obtained in healthy female controls.

In cases 5 and 7, we examined for the items for which they retrieved a pathologically (< 1 SD) low number of visual features and which were also part of the confrontation naming task, whether these were named accurately and expediently. For all 7 items investigated, naming accuracy and voice onset reaction times were well within the normal range except for one item which case 5 named more slowly (Table 7).

Inversely, in cases 1-4, who were impaired on confrontation naming, we examined feature generation for those items which they failed to name correctly and which were also tested during feature generation. For all items investigated, the proportion of visual features was well within the normal range except for one item for which case 3 retrieved less visual features than normal controls (Table 7).

Items for which feature generation was impaired				
case	item	voice onset RT	Controls: mean	S.D.
case 5	giraffe	**2314**	1524	313
case 5	cow	1705	1755	609
case 5	apple	1268	2132	732
case 7	apple	1314	id.	id.
case 5	melon	1502	2700	986
case 7	frog	1310	1858	699
case 7	wrench	1654	3692	2780
Items for which naming was impaired				
		proportion of visual features	Controls: mean	S.D.
case 1	melon	0.300	0.357	0.206
case 2	melon	0.167	id.	id.
case 3	melon	0.500	id.	id.
case 2	lettuce	0.125	0.163	0.133
case 3	sled	**0**	0.189	0.144
case 4	wrench	0.364	0.272	0.165

Table 7 – Reaction times for those items in which either feature generation or naming was pathological and which were also tested in the naming or feature generation task, respectively. Voice onset reaction times: Bold: one-tailed $P<0.05$ compared to healthy controls. Feature generation: Bold: more than 1 S.D. below mean of normal controls. Id.: same value as cell above.

4. Discussion

A lesion confined to right medial fusiform cortex (Fig. 1) caused a naming deficit for tools, which is unique in the literature to the best of our knowledge (Table 4, case 4). More globally, across the entire group, impairment organized along a categorical line dissociated from impairment organized along the dimension of attribute type (Table 4 cases 1, 2 & 4, Table 6 cases 5 & 7).

The onset time and slope of the speeded identification is a sensitive manner to evaluate visuoperceptual processing for words and pictures. In case 1-3, the slope of the picture identification curve was abnormal (Fig. 2), indicative of a reduced visuoperceptual processing speed Bundesen (1990). This may well contribute to the category-specific naming deficit as identification of biological items tends to pose higher visuoperceptual demands than nonbiological items. In line with Capitani et al. (2009), the cases with a category-specific naming deficit for biological entities (case 1, 2) had the largest lesions which also extended more anteriorly. Feature statistics and a computational approach may offer an explanation for the possible association between lesion extent, visuoperceptual identification problems and category-specificity. Biological entities are perceptually more similar to each other than nonbiological entities (Humphreys and Riddoch, 1987), have more shared features and fewer distinctive features according to feature generation data, and the distinctive features correlate with each other to a lesser degree than is the case for non-biological entities (Moss et al., 1998; Randall et al., 2004; Taylor et al., 2012). These differences render visuoperceptual identification of biological entities more demanding than that of nonbiological entities, which may explain why larger lesions of the occipitotemporal pathway affect biological entities more than non-biological entities. Based on computer simulations, higher similarity between biological entities would make them more vulnerable to damage of the computational network and cause the concepts to be harmed together (Rogers et al., 2004).

Both patients and controls retrieved more functional-associative attributes than visual attributes (Table 6). This differs from what has been reported in most other types of tasks probing knowledge about concrete entities. A characteristic of our task is the fixed, one-minute duration for each of the 60 items. This leads to a more exhaustive search so that less salient features are also generated compared to tasks where subjects spend less time on each single item (e.g. a total of approximately 400 entities in 40-45 min (Vinson and Vigliocco, 2002)). Given the long duration per entity, the proportion of visual versus functional-associative attributes may also differ from what one would derive based on judgements of the weight subjects attribute to features (Gainotti et al., 2009, 2013; Hoffman and Lambon Ralph, 2013). An advantage of the longer duration is that subjects may direct attention to properties that would otherwise not be thought of or mentioned, possibly reflecting property knowledge in a more complete manner.

A disproportionate deficit in retrieving visual-sensory attributes compared to functional-associative attributes occurred in two cases who did not have a category-specific defect (case 5, 7) (Table 3; Table 6A-C). These cases had relatively small lesions (Figure 1, Table 1). The lesion in case 5 fell within the boundaries of JA's lesion, although it was much smaller (Vandenbulcke et al., 2006). In case JA, we observed an absolute deficit in generating visual attributes, whereas in cases 5 and 7, the deficit was relative and only observed when correcting for the total number of generated features (Table 6B). JA was also impaired on naming-to-definition when the definitions were based on visual-sensory rather than functional-associative attributes and on drawing-from-memory with preserved copy (Vandenbulcke et al., 2006). Furthermore, JA was impaired on the Object Decision task and had a reduced slope on the speeded word and picture identification task for biological and nonbiological entities (Vandenbulcke et al., 2006). Taken together, this combination of test results led us to situate JA's deficit at the level of the structural description system (Forde et al., 1997; Humphreys and Forde, 2001). Given the preservation of speeded word and picture identification (Table 2, Fig. 2), a structural description processing deficit can be excluded as an explanation in the current cases. Possibly, the change in proportion of visual attributes generated follows from a change in mental imagery (Kosslyn et al., 1999; Kosslyn and Thompson, 2003). For instance, a lesion of primary visual cortex as observed in case 7 may lead to a general shift in search strategy towards nonvisual domains or a selective change in attention away from visual attributes during mnemonic retrieval. Alternatively the mental images of concrete objects may be more 'blurred' due to the lesion so that their visual attributes become more difficult to access. The effect may also be mediated by functional effects at a distance from the structural lesion due to de-afferentation.

It is worth noting that retrieval of visual-sensory attributes was most impaired for biological entities, especially in case 7 (Table 6A-C). Similar interactions between task and attribute type have been described in the past (Sartori and Job, 1988; DeRenzi and Lucchelli, 1994; Gainotti and Silveri, 1996). As processing of biological entities is weighted more heavily towards visual-sensory rather than functional-associative attributes (Garrard et al., 2001; Sartori and Lombardi, 2005), a deficit in retrieving visual-sensory attributes may be most evident when testing the biological category. According to the sensory-functional hypothesis, disproportionate impairment for biological entities is attributable to this heavier reliance on visual processing pathways (Warrington and Shallice, 1984; Shallice, 1987). This hypothesis leads one to predict that a category-specific deficit for biological items should be associated with a disproportionate decrease in retrieval of visual compared to functional-associative attributes *regardless* of category (Sartori and Job, 1988). Our data did not confirm this prediction, in line with numerous other studies (Laiacona et al., 1993, 1997; Moss et al., 1998; Lambon Ralph et al., 1998; Mahon et al., 2009; Capitani et al., 2009; Mahon and Caramazza, 2011): we observed category-specific deficits in cases who were not impaired on retrieval of visual attributes (cases 1-3) and, inversely, a deficit in retrieval of visual attributes (case 5, 7) occurred in the absence a category-specific deficit. Other cases have been reported who exhibit impaired retrieval of visual attributes in the absence of category-specificity (e.g. JA by Vandenbulcke et al. (2006) and AC by Coltheart et al. (1998)).

To the best of our knowledge, a category-specific deficit for non-biological entities (Table 4 case 4) has not been reported before with a right-sided PCA lesion. Lesions restricted to medial fusiform cortex (Fig. 1, 4) are highly exceptional given the human brain arterial territory distribution. In case 4 the lesion was caused by a venous thrombosis. Case 4 was principally impaired for tools, with paraphasias consisting of other tools or neologisms referring to the affordances of the tool picture. Previous studies have pointed to potential gender effects on category-specific deficits, possibly because of gender-dependent differences in familiarity (Gainotti, 2005). We did not find a gender effect in our feature generation or naming task. When we compared case 4 to a control group of women only, the tool naming deficit remained significant. Our primary research question related to changes in retrieval of visual attributes as a consequence of occipitotemporal lesions. For that reason, we primarily classified the attributes into three classes: visual, nonvisual sensory, and functional-associative. Specifically in case 4, in order to get more insight into her deficit naming tools, we further distinguished within the broad 'functional-associative' class between properties generated in relation to function and manipulability (Buxbaum et al., 2000; Buxbaum and Saffran, 2002; Boronat et al., 2005) and compared her performance to that by the female controls. Verbally cued knowledge about tools was preserved for these different dimensions. This would suggest that the deficit was situated at the level of recognition of tools as compared to animate entities or, less likely, connecting the tool concept with its lexical label.

As far as we are aware, all other instances in whom an impairment of artifacts was reported, were due to either left-sided (Hillis and Caramazza, 1991; Tippett et al., 1996; Silveri et al., 1997; Sacchett and Humphreys, 1992) or bilateral lesions (Warrington and McCarthy, 1994). Both temporal (Hillis and Caramazza, 1991; Tippett et al., 1996) and frontoparietal lesion sites (Sacchett and Humphreys, 1992) have been reported. In a right-sided lesion case (SM) who had a relatively extensive PCA lesion Turnbull and Laws (2000), nonbiological entities were more affected than biological entities only when the analysis was restricted to the low-familiarity items (principally driven by musical instruments versus animals) (Turnbull and Laws, 2000). This resulted in an interaction between category and familiarity rather than a main effect of category (Turnbull and Laws, 2000).

The localisation of the lesion in case 4 (Figure 1) fits remarkably well with the medial fusiform activation observed in PET or fMRI when tools are compared to other categories (Chao et al., 1999, 2002; Devlin et al., 2005; Mechelli et al., 2006) (Figure 4). The coordinate obtained when contrasting naming of tools versus animals reported by Chao et al. (2002) lies at the centre of the small lesion in right medial fusiform gyrus in case 4 (Figure 4). This region is also activated for tools compared to animate entities during experimental conditions, such as passive viewing, property verification (Chao et al., 1999, 2002) or semantic decision (Devlin et al., 2005) (Figure 4).

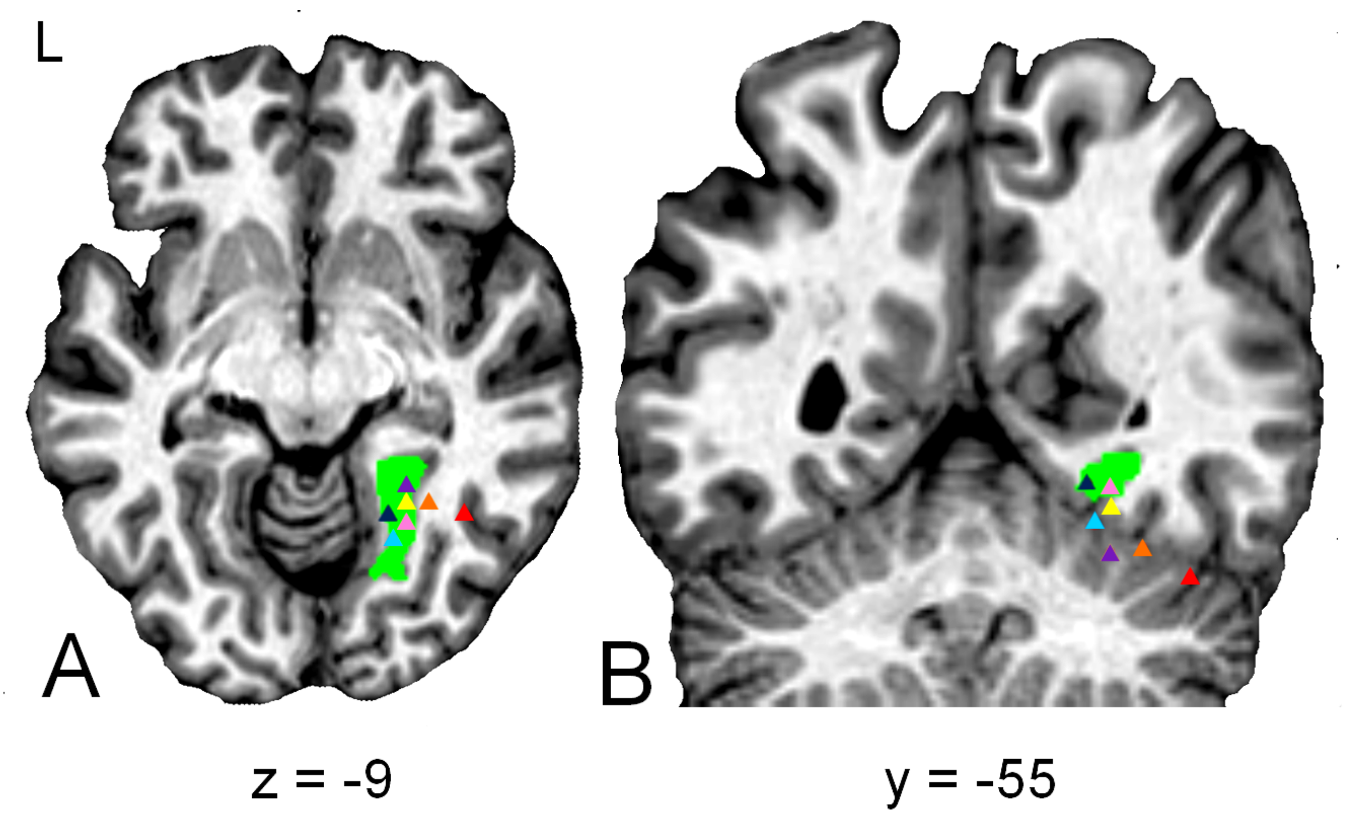

Figure 4 – Neuroanatomical relationship between the lesion volume of case 4 and fMRI activations of tools versus animals from the literature: A. Axial section showing the extent of the lesion at z = -9 mm (green). This section provides a see-through projection of activity peaks from z= 27 to -9 mm. This panel provides a view of how lesion volume relates to activity peaks from the literature along the x and y dimensions, while disregarding the z dimension. **B.** Coronal section showing the extent of the lesion at y = 55 mm (green). This section provides a see-through projection of activity peaks from y = -48 to 60 mm. This panel provides a view of how lesion volume relates to activity peaks from the literature along the x and z dimensions, while disregarding the y dimension. **Legend**: Triangles refer to activity peaks from the literature. *Cyan*: reading names of tools versus animals (Chao et al., 1999) (Talairach (Tal.) coordinates x = 23, y = -59, z = -11). *Yellow*: passive viewing of tools versus animals (Chao et al., 1999) (Tal. x = 26, y = -48, z = -9). *Purple*: naming of tools versus animals (Chao et al., 1999) (Tal. x = 26, y = -47, z = -16). *Dark blue*: naming of tools and animals (Chao et al., 2002) (Tal. x = 22, y = -54, z = -5). *Pink*: perceptual and semantic decisions on man-made entities versus natural entities (Devlin et al., 2005) (MNI coordinates x = 26, y = -56, z = -10). *Orange*: naming of artefacts versus animals, (Mechelli et al., 2006) (Tal. x = 32, y = -50, z = -16). *Red*: matching tools versus animals (Chao et al., 1999) (Tal. 41, -53, -20).

The neurobiological processes that underly the selectivity of this region for tools are still under investigation and a variety of experiments have been conducted to evaluate different theoretical models that could account for such selectivity. In case 4 the speeded visuoperceptual identification slope and onset time were intact both for pictures and for words, ruling out a general visuoperceptual deficit or object-based hemineglect as that would lead to slowing of identification of foveal pictures or words or laterality biases in the speeded word identification. Feature statistics as derived from a concept-feature matrix may provide important clues in this respect. For instance, the fMRI response evoked by tools in medial fusiform cortex is modulated by 'semantic relevance', which is calculated from a nonlinear combination of distinctiveness and dominance (Sartori and Lombardi, 2004; Mechelli et al., 2006). Distinctiveness reflects the frequency with which a feature is mentioned over the different concepts and is the inverse of 'sharedness' (Moss et al., 1998; Tyler et al., 2013) while dominance reflects how readily a given feature is provided for that concept (Mechelli et al., 2006). Artefacts with features scoring high on semantic relevance activate right medial fusiform cortex more than artefacts who score lower and also more than biological entities (Mechelli et al., 2006). While feature statistics appear to explain the tool-selectivity of medial fusiform cortex to some degree, the neurophysiological origin of these effects remain unclear. Alternative explanations remain possible. For instance, identification of tools may rely more on spatial relationships between object parts and how these change when the object is held in different positions during object use (Sacchett and Humphreys, 1992). This may differ from biological entities who are presented relatively more often according to a standard spatial reference frame determined by the gravitational vertical (Sacchett and Humphreys, 1992). Theoretically, such spatial processing during object identification may depend more on medial fusiform gyrus.

To conclude, right PCA lesions are associated with a variety of patterns of deficits in naming and feature generation tasks. Within our dataset this appears to be determined not only by the site but also by the extent of the damage: large lesions that extend anteriorly and are associated with visuoperceptual identification problems cause a naming deficit for biological entities, small lesions that are confined to early visual regions cause a feature generation deficit for visual-sensory attributes in particular for biological entities. Uniquely, a lesion confined to right medial fusiform cortex was associated with a deficit in naming tools. The lesion data confirm for the first time the critical role of right medial fusiform cortex in tool naming (Chao et al., 1999, 2002).

5. References

Boronat, C. B., Buxbaum, L. J., Coslett, H. B., Tang, K., Saffran, E. M., Kimberg, D. Y., and Detre, J. A. (2005). Distinctions between manipulation and function knowledge of objects: evidence from functional magnetic resonance imaging. *Brain Res Cogn Brain Res*, 23(2-3):361–373.

Bruffaerts, R., Dupont, P., Peeters, R., De Deyne, S., Storms, G., and Vandenberghe, R. (2013). Similarity of fmri activity patterns in left perirhinal cortex reflects semantic similarity between words. *J Neurosci*, 33(47):18597–18607.

Bundesen, C. (1990). A theory of visual attention. *Psychol. Rev.*, 97:523–547.

Buxbaum, L. J. and Saffran, E. M. (2002). Knowledge of object manipulation and object function: dissociations in apraxic and nonapraxic subjects. *Brain Lang*, 82(2):179–199.

Buxbaum, L. J., Veramonti, T., and Schwartz, M. (2000). Function and manipulation tool knowledge in apraxia: Knowing 'what for' but not 'how'. *Neurocase*, 6:83–97.

Capitani, E., Laiacona, M., Mahon, B., and Caramazza, A. (2003). What are the facts of semantic category-specific deficits? a critical review of the clinical evidence. *Cogn Neuropsychol*, 20(3):213–261.

Capitani, E., Laiacona, M., Pagani, R., Capasso, R., Zampetti, P., and Miceli, G. (2009). Posterior cerebral artery infarcts and semantic category dissociations: a study of 28 patients. *Brain*, 132(Pt 4):965–981.

Chao, L., Haxby, J., and Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci*, 2:913–919.

Chao, L., Weisberg, J., and Martin, A. (2002). Experience dependent modulation of category-related cortical activity. *Cerebral Cortex*, 12:545–551.

Coltheart, M., Inglis, L., Cupples, L., Michie, P., Bates, A., and Budd, B. (1998). A semantic subsystem of visual attributes. *Neurocase*, 4:353–370.

Crawford, J. and Garthwaite, P. (2005). Testing for suspected impairments and dissociations in single-case studies in neuropsychology: Evaluation of alternatives using Monte Carlo simulations and revised tests for dissociations. *Neuropsychology*, 19:318–331.

Crawford, J. R., Garthwaite, P. H., and Gray, C. D. (2003). Wanted: fully operational definitions of dissociations in single-case studies. *Cortex*, 39(2):357–370.

Cree, G. S. and McRae, K. (2003). Analyzing the factors underlying the structure and computation of the meaning of chipmunk, cherry, chisel, cheese, and cello (and many other such concrete nouns). *J Exp Psychol Gen*, 132(2):163–201.

De Deyne, S. and Storms, G. (2008a). Word associations: network and semantic properties. *Behav Res Methods*, 40(1):213–231.

De Deyne, S. and Storms, G. (2008b). Word associations: norms for 1,424 dutch words in a continuous task. *Behav Res Methods*, 40(1):198–205.

De Deyne, S., Verheyen, S., Ameel, E., Vanpaemel, W., Dry, M. J., Voorspoels, W., and Storms, G. (2008). Exemplar by feature applicability matrices and other dutch normative data for semantic concepts. *Behav Res Methods*, 40(4):1030–1048.

DeRenzi, E. and Lucchelli, F. (1994). Are semantic systems separately represented in the brain? the case of living category impairment. *Cortex*, 30:3–25.

Devlin, J. T., Rushworth, M. F. S., and Matthews, P. M. (2005). Category-related activation for written words in the posterior fusiform is task specific. *Neuropsychologia*, 43(1):69–74.

Farah, M., McMullen, P., and Meyer, M. (1991). Can recognition of living things be selectively impaired? *Neuropsychologia*, 29:185–193.

Flores d'Arcais, G., Schreuder, R., and Glazenborg, G. (1985). Semantic activation during recognition of referential words. *Psychological Research*, 47:39–49.

Forde, E., Francis, D., Riddoch, M., Rumiati, R., and Humphreys, G. (1997). On the links between visual knowledge and naming: a single case study of a patient with a category-specific impairent for living things. *Cognitive Neuropsychology*, 14:403–458.

Gainotti, G. (2000). What the locus of brain lesion tells us about the nature of the cognitive defect underlying category-specific disorders: A review. *Cortex*, 36:539–559.

Gainotti, G. (2005). The influence of gender and lesion location on naming disorders for animals, plants and artefacts. *Neuropsychologia*, 43(11):1633–1644.

Gainotti, G., Ciaraffa, F., Silveri, M. C., and Marra, C. (2009). Mental representation of normal subjects about the sources of knowledge in different semantic categories and unique entities. *Neuropsychology*, 23:803–812.

Gainotti, G. and Silveri, M. (1996). Cognitive and anatomical locus of lesion in a patient with a category-specific semantic impairment for living things. *Cognit Neuropsychology*, 13:357–389.

Gainotti, G., Spinelli, P., Scaricamazza, E., and Marra, C. (2013). The evaluation of sources of knowledge underlying different conceptual categories. *Front Hum Neurosci*, 7:40.

Garrard, P., Ralph, M. A., Hodges, J. R., and Patterson, K. (2001). Prototypicality, distinctiveness, and intercorrelation: Analyses of the semantic attributes of living and nonliving concepts. *Cogn Neuropsychol*, 18(2):125–174.

Hankey, J., Young, A., and N., P. (1989). Defective recognition of familiar people. *Cognitive Neuropsychology*, 6:179–210.

Hillis, A. and Caramazza, A. (1991). Category-specific naming and comprehension impairment: A double dissociation. *Brain*, 114:2081–2094.

Hoffman, P. and Lambon Ralph, M. A. (2013). Shapes, scents and sounds: quantifying the full multi-sensory basis of conceptual knowledge. *Neuropsychologia*, 51(1):14–25.

Humphreys, G. and Forde, E. (2001). Hierarchies, similarity and interactivity in object recognition. *Behav. Brain Sci.*, 24:453–476.

Humphreys, G. and Riddoch, M. (1987). On teltell your fruit from your vegetavege: a consideration of category-specific deficits after brain damage. *Trends in Neuroscience*, 10:145–148.

Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J., Ganis, G., Sukel, K., Alpert, N., et al. (1999). The role of area 17 in visual imagery: convergent evidence from pet and rtms. *Science*, 284(5411):167–170.

Kosslyn, S. M. and Thompson, W. L. (2003). When is early visual cortex activated during visual mental imagery? *Psychological bulletin*, 129(5):723.

Laiacona, M., Barbarotto, R., and Capitani, E. (1993). Perceptual and associative knowledge in category-specific impairment of semantic memory: A study of two cases. *Cortex*, 29:727–740.

Laiacona, M. and Capitani, E. (2001). A case of prevailing deficit of nonliving categories or a case of prevailing sparing of living categories. *Cognitive Neuropsychology*, 18:39–70.

Laiacona, M., Capitani, E., and Barbarotto, R. (1997). Semantic category dissociations: A longitudinal study of two cases. *Cortex*, 33:441–446.

Lambon Ralph, M. A., Howard, D., Nightingale, G., and Ellis, A. W. (1998). Are living and non-living category-specific deficits causally linked to impaired perceptual or associative knowledge? evidence from a category-specific double dissociation. *Neurocase*, 4(4-5):311–338.

Mahon, B. Z., Anzellotti, S., Schwarzbach, J., Zampini, M., and Caramazza, A. (2009). Category-specific organization in the human brain does not require visual experience. *Neuron*, 63(3):397–405.

Mahon, B. Z. and Caramazza, A. (2011). What drives the organization of object knowledge in the brain? *Trends Cogn Sci*, 15(3):97–103.

Mechelli, A., Sartori, G., Orlandi, P., and Price, C. J. (2006). Semantic relevance explains category effects in medial fusiform gyri. *Neuroimage*, 30(3):992–1002.

Molenberghs, P., Gillebert, C. R., Peeters, R., and Vandenberghe, R. (2008). Convergence between lesion-symptom mapping and functional magnetic resonance imaging of spatially selective attention in the intact brain. *J Neurosci*, 28(13):3359–3373.

Moss, H. E., Tyler, L. K., Durrant-Peatfield, M., and Bunn, E. M. (1998). two eyes of a see-through: Impaired and intact semantic knowledge in a case of selective deficit for living things. *Neurocase*, 4(4-5):291–310.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9:97–113.

Randall, B., Moss, H. E., Rodd, J. M., Greer, M., and Tyler, L. K. (2004). Distinctiveness and correlation in conceptual structure: behavioral and computational studies. *J Exp Psychol Learn Mem Cogn*, 30(2):393–406.

Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., and Patterson, K. (2004). Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychol Rev*, 111(1):205–235.

Rorden, C., Karnath, H., and Bonilha, L. (2007). Improving lesion-symptom mapping. *J Cognit Neurosci*, 19:1081–1088.

Ruts, W., De Deyne, S., Ameel, E., Vanpaemel, W., Verbeemen, T., and Storms, G. (2004). Dutch norm data for 13 semantic categories and 338 exemplars. *Behav Res Methods Instrum Comput*, 36(3):506–515.

Sacchett, C. and Humphreys, G. (1992). Calling a squirrel a squirrel but a canoe a wigwam: a category-specific deficit for artefactual objects and body part. *Cognitive Neuropsychology*, 9:73–86.

Sartori, G. and Job, R. (1988). The oyster with four legs: A neuropsychological study on the interaction between vision and semantic information. *Cognitive Neuropsychology*, 5:105–132.

Sartori, G. and Lombardi, L. (2004). Semantic relevance and semantic disorders. *Journal of Cognitive Neuroscience*, 16(3):439–452.

Sartori, G. and Lombardi, L. (2005). Double dissociations on the same stimuli. *Cortex*, 41(6):867–8; discussion 869–72.

Shallice, T. (1987). Impairments of semantic processing: multiple dissociations. In Coltheart, M., Sartori, G., and Job, R., editors, *The cognitive neuropsychology of language*, pages 111–127. Lawrence Erlbaum Associates, Hove and London.

Shallice, T. (1988). *From neuropsychology to mental structure.* Cambridge: Cambridge University Press.

Silveri, M. C., Gainotti, G., Perani, D., Cappelletti, J. Y., Carbone, G., and Fazio, F. (1997). Naming deficit for non-living items: neuropsychological and pet study. *Neuropsychologia*, 35(3):359–367.

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

Taylor, K. I., Devereux, B. J., Acres, K., Randall, B., and Tyler, L. K. (2012). Contrasting effects of feature-based statistics on the categorisation and basic-level identification of visual objects. *Cognition*, 122(3):363–374.

Tippett, L. J., Glosser, G., and Farah, M. J. (1996). A category-specific naming impairment after temporal lobectomy. *Neuropsychologia*, 34(2):139–146.

Turnbull, O. and Laws, K. (2000). Loss of stored knowledge of object structure: implications for ”category-specific” deficits. *Cognitive Neuropsychology*, 17:365–389.

Tyler, L. K., Chiu, S., Zhuang, J., Randall, B., Devereux, B. J., Wright, P., Clarke, A., and Taylor, K. I. (2013). Objects and categories: feature statistics and object processing in the ventral stream. *J Cogn Neurosci*, 25(10):1723–1735.

Vandenbulcke, M., Peeters, R., Dupont, P., Van Hecke, P., and Vandenberghe, R. (2007). Word reading and posterior temporal dysfunction in amnestic mild cognitive impairment. *Cereb. Cortex*, 17:542–551.

Vandenbulcke, M., Peeters, R., Fannes, K., and Vandenberghe, R. (2006). Knowledge of visual attributes in the right hemisphere. *Nat. Neurosci.*, 9:964–970.

Verhaeghen, P., Vandenbroucke, A., and Dierckx, V. (1998). Growing slower and less accurate: Adult age differences in time-accuracy functions for recall and recognition from episodic memory. *Exp Aging Res*, 24:3–19.

Vinson, D. P. and Vigliocco, G. (2002). A semantic analysis of grammatical class impairments: semantic representations of object nouns, action nouns and action verbs. *Journal of Neurolinguistics*, 15:317–351.

Warrington, E. and McCarthy, R. (1994). Multiple meaning systems in the brain: a case for visual semantics. *Neuropsychologia*, 32:1465–1473.

Warrington, E. and Shallice, T. (1984). Category specific semantic impairments. *Brain*, 107:829–853.