



When the zebra loses its stripes but is still in the savannah: Results from a semantic priming paradigm in semantic dementia



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ABSTRACT

Studies using semantic priming paradigms to measure the integrity of the features underlying concepts in semantic dementia (SD) reported differential impairment, in that functional features appeared to be more robust to brain damage than other features, such as perceptual ones. However, these prior studies were single case reports and the inclusion of too many heterogeneous features under the “functional features” heading casts doubts on their apparent preservation. To verify the robustness of functional features compared with perceptual ones, we carried out a group study where we deliberately restricted the exploration of semantic features to two clearly defined types of attribute: visuoperceptual (“visual”) versus contextual–functional (“contextual”). We administered an implicit lexical-decision priming task to 8 SD patients and 31 healthy matched controls, at baseline. Four of the patients underwent a follow-up assessment at one year. For controls, we found a significant priming effect in the visual condition, but not in the contextual one, whereas the SD group exhibited the reverse pattern of performances. The follow-up data provided evidence of the robustness of the dissociation between priming performances in the two attribute conditions. The fact that a particular priming effect was observed in the SD patients but not in controls could be regarded as a sign of semantic disequilibrium. Since perceptual features have been shown to be a core determinant of similarity-based/taxonomic relationships, whereas complementary-based/thematic processing relies mainly on contextual relationships, we interpreted our findings in terms of the differential recruitment of one of the two systems of semantic relationships (taxonomic vs. thematic). Moreover, these two distinct and parallel systems have previously been reported to coexist – and compete – in healthy adults. We thus argue that controls automatically drew on similarity-based/taxonomic relationships, leading to a significant priming effect for visual features but not for contextual ones. By contrast, their impaired perceptual features forced the SD patients to resort to the system of thematic relationships.

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1. Introduction

Semantic dementia (SD) is a rare subtype of frontotemporal lobar degeneration (Moreaud et al., 2008; Neary et al., 1998; Snowden, Goulding, & Neary, 1989). It arises out of temporal lobe atrophy, often bilateral but predominantly on the left side (Chan et al., 2001; Hodges, Patterson, Oxbury, & Funnell, 1992). SD is characterized by a gradual and a selective loss of conceptual knowledge, resulting in limited vocabulary in speech, poor

comprehension, and deficits in the identification of objects and persons in different input modalities (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Luzzi et al., 2007; Snowden, Thompson, & Neary, 2004). While conceptual knowledge distressingly collapses as the disease progresses, language remains fluent and well-structured, without any phonological or grammatical errors, and only subtle abnormalities in the syntactic structure of SD patients' speech have been reported (Meteyard & Patterson, 2009). General intellectual ability, day-to-day memory and visuo-perceptual abilities remain relatively spared. Activities of daily living are also relatively preserved until the later stages of the disease.

Semantic breakdown in SD is currently presented as “a selective impairment to semantic abilities that affects all modalities of

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reception and expression, for all kinds of concepts, more or less equally, and it is the consequence of relatively focal brain lesions” (Patterson, Nestor, & Rogers, 2007, p. 978). Although SD patients often exhibit a significant deterioration in the attributes of underlying concepts, Lambon Ralph, Patterson, Garrard, and Hodges (2003) used explicit semantic tasks (naming to description, description-to-picture matching, and verbal definitions) to show that functional/associative features fare better than sensory/perceptual ones.

Patients' performances on explicit semantic tasks could, however, potentially be biased by the activation of intentional and deliberate processes (Ober, 2002), thus increasing the probability of impairment due to extra-semantic processes. For this reason, it is advisable to use an implicit assessment when exploring the organization of conceptual knowledge. Semantic priming paradigms are one of the methods that are currently used to measure the integrity of semantic knowledge. Priming tasks reduce intentional processes and promote automatic access to semantic knowledge. Operationalized in a lexical-decision task, these implicit paradigms require participants to decide as quickly and as accurately as possible whether a letter string constitutes a real word. This word is preceded by the brief presentation of a prime word that is either related or unrelated semantically to the target word. Based on spreading activation theory, and its assumptions of an interconnected network of concepts (Collins & Loftus, 1975), these paradigms trigger the automatic activation of all the concepts connected to the prime word, such that short reaction times (RTs) can be assumed to reflect closeness between concepts (i.e., between the prime and target words) in the semantic network.

To our knowledge, only five studies have used priming paradigms, operationalized in implicit lexical-decision tasks to measure the integrity of semantic knowledge in SD patients (Laisney et al., 2011; Moss, Tyler, Patterson, & Hodges, 1995a; Nakamura, Nakanishi, Hamanaka, Nakaaki, & Yoshida, 2000; Rogers & Friedman, 2008; Tyler & Moss, 1998). In most of these studies, the primed monitoring tasks explored different kinds of semantic relations between concepts, comparing category superordinates/coordinates with unspecified attributes or functional features within the same experimental design.

Disturbed priming effects were reported when the implicit assessment focused on category superordinate (e.g., “walnut” priming “wood”) and/or coordinate relationships (e.g., “cherry” priming “apple”). Three studies failed to demonstrate any priming effect at all in these conditions (Moss et al., 1995a; Nakamura et al., 2000; Rogers & Friedman, 2008), while Laisney et al. (2011) observed an abnormally increased priming effect in the two category-coordinate conditions (distant coordinate relationships: “whale” priming “shark”; and close coordinate relationships: “bee” priming “wasp”). Moreover, the magnitude of this hyperpriming effect was greater for close coordinate conditions than for distant ones. This last result was underpinned by the extinction of the semantic priming effect in the distinctive attribute condition in the SD group (e.g., “zebra” priming “stripes”). In accordance with Chertkow, Bub, and Seidenberg (1989), Laisney et al. (2011) interpreted this hyperpriming effect as the result of disturbed semantic knowledge. More specifically, they regarded it as reflecting the loss of distinctive attributes. Since the prime and the target could no longer be distinguished, an over-priming condition was generated (Giffard et al., 2001, 2002). In a longitudinal study in Alzheimer's disease (AD), Giffard et al. (2002) found that the hyperpriming effect was purely transient, corresponding to a narrow window of opportunity as the semantic system continued to deteriorate. The extensive semantic knowledge loss subsequently spread to every feature of the concepts, with the result that priming effects could no longer be observed in any of the conditions.

Priming studies assessing attribute integrity in SD patients have yielded rather conflicting results, leading to divergent conclusions regarding the deterioration in semantic features. While two earlier case reports (Moss et al., 1995a; Tyler & Moss, 1998) had highlighted a surprising preservation of the priming effect in the functional attribute condition in two SD patients (PP and AM), two later studies (Laisney et al., 2011; Rogers & Friedman, 2008) failed to find any priming effect in attribute conditions in SD groups. These apparently conflicting results may stem from the fact that these two recent studies were not designed to compare the integrity of different kinds of features. Moreover, Rogers and Friedman (2008) did not provide any details about the types of features they used. Studies making a more fine-grained distinction between different types of attributes have reported differential priming patterns. In the first case study (Moss et al., 1995a), PP exhibited spared semantic priming for functional features (e.g., “shampoo” priming “hair”), but no priming effect for category-coordinate relationships (e.g., “cat” priming “dog”). In the second case study, Tyler and Moss (1998) assessed the integrity of two kinds of features (functional: “crocodile” priming “river”; and perceptual: “crocodile” priming “green”) and two category relations (superordinate: “crocodile” priming “animal”; and coordinate: “crocodile” priming “alligator”). AM underwent the same testing session three times over an 18-month period. On initial testing, AM showed normal priming effects in the two attribute conditions, but no priming in the category conditions. At the 11-month follow up, functional attributes continued to prime robustly, but priming was no longer observed in the other conditions, including perceptual attributes.

Nonetheless, various methodological shortcomings may partially account for the longer preservation of priming effects in the functional condition. One could argue that the features included under the heading of so-called “functional properties” in the experiments conducted by Moss et al. (1995a) and Tyler and Moss (1998) were heterogeneous. In the former, Moss et al. (1995a) combined two kinds of relationships in the functional condition: a set of priming pairs where the prime consisted in something that was used to perform an action on the target (e.g., “broom” – “floor”) and another set of priming pairs sharing contextual relationships (i.e., frequent co-occurrence, with the target referring to a typical component of the event or script evoked by the prime: “theater” – “play”). In Tyler and Moss's (1998) priming task, this heterogeneity was even more striking since a careful examination of the kinds of features included in the functional condition highlighted quite different kinds of relationships between the primes and the targets. Under the same « functional » label, the primes and the targets could in fact share “used to perform an action” relationships (e.g., “desk” priming “work”), contextual relationships (e.g., “crocodile” priming “river”), as well as word pairs containing strong lexical associations, i.e. relationships between two concepts in idiomatic expressions, proverbs and quotations (e.g., “fox” priming “sly”). Such heterogeneity makes it hard to draw inferences about the status of so-called “functional” features. Indeed, Rogers and Friedman (2008) have claimed that the lexical associations involve nonsemantic processing. In their semantic priming task, they included this kind of relationship as a control condition (e.g., “needle” priming “haystack”) and observed a normal priming effect in SD patients. Moreover, “used to perform an action” relationships could, to some extent, implicate the visual object affordances (i.e., mechanisms that support object use directly from visual and/or tactile input) which were isolated by Hodges, Bozeat, Lambon Ralph, Patterson, and Spatt (2000) as one of the factors accounting for spared abilities to use objects in SD. We could thus ascribe the spared and robust priming effect previously observed in SD patients to the excessively broad types of attributes included

Table 1
SD patients' and controls' demographic and clinical features.

	Controls		SD patients								
	Mean (standard deviation)	Range	SD1	SD2	SD3	SD4	SD5	SD6	SD7	SD8	Mean (standard deviation)
Sex (female; male)	20 F; 11 M		F	F	M	F	M	F	F	F	6 F; 2 M
Age (years)	62.8 (4.8)	56–72	64	62	69	58	66	63	75	64	65.1 (5.1)
Handedness (L=left; R=right)	1 L; 30 R		R	R	L	R	R	L	R	R	2 L; 6 R
Education (years)	12.1 (4.1)	7–21	9	9	14	12	12	19	9	8	11.5 (3.7)
Disease duration (months)			27	32	11	17	3	16	13	1	15 (10.7)
Side of atrophy (L=left; B=bilateral; R=right)			B	B	B	L	B	R	L	L	(3 L; 4B; 1 R)

under the label “functional condition”. This lack of boundary lines between attributes could yet be expected, given the theoretical account underpinning their study. Indeed, Tyler and Moss (1998) compared perceptual versus functional features in relation to sensory/functional theory (SFT; Warrington & Shallice, 1984). This theoretical account assumes that semantic memory is divided into two subsystems, where knowledge about concepts is topographically organized according to the properties that are most distinctive for a given domain (living vs. nonliving concepts). More specifically, SFT predicts that the identification of living entities depends mainly on sensory features, whereas functional features are critical for the representation of nonliving items. This theory is inherently flawed, in that it is hard to find functional attributes that are equally salient for both living and nonliving entities. This problem had led to the extension of functional properties to associative features and encyclopedic knowledge for living entities (Tyler & Moss, 1997). Tyler and Moss's (1998) reference to SFT could thus explain the apparent heterogeneity within their set of functional attributes. Moreover, we identified another methodological bias in Tyler and Moss's (1998) study that could account for the robustness of functional features since the set of targets in that priming condition contained both nouns and verbs (e.g., “cherry” priming “eat”). Action verbs processing was yet demonstrated to rely on frontal-subcortical circuits (Davis et al., 2010) and to be virtually preserved in SD (Silveri, Perri, & Cappa, 2003).

In the present study, we sought to investigate the nature of semantic disorders in SD patients by means of an implicit lexical-decision priming task, focusing our analysis on two different types of attributes: visuoperceptual (“visual”) versus contextual-functional (“contextual”). The purpose of the study was thus to verify the robustness of functional features compared with visual ones in a group of SD patients and after limiting the features included under the functional heading to one clearly defined subtype (i.e., contextual relations between two entities). Contextual attributes had the added advantage of being easier to find for both living and nonliving concepts.

A second goal was to determine whether this hypothetically differential deterioration in perceptual versus functional features persists as the disease progresses, by conducting a second assessment of patients at one-year follow up.

2. Methods

2.1. Participants and background data

2.1.1. Semantic dementia

Eight patients who met the diagnostic criteria for SD (Neary et al., 1998) were included in this study after providing their written informed consent. All of them were native French speakers and were followed at the memory clinic of Rennes University Hospital (see Table 1 for individual demographic and clinical features).

To establish their cognitive profile, we administered a comprehensive neuropsychological battery to the SD patients in a separate session just before they carried out the experimental task (see Table 2 for individual scores). This neuropsychological battery consisted of an assessment of their general cognitive functioning

(Raven's Colored Progressive Matrices, RCPM; Raven, Raven, & Court, 1998; Dementia Rating Scale, DRS; Mattis, 1976), working memory (digit span forward and backward, Wechsler Adult Intelligence Scale-Revised, WAIS-R; Wechsler, 1981), nonverbal episodic memory (“La Roche” visuospatial learning task; Violon & Wijns, 1984; delayed recall of the Rey-Osterrieth Complex Figure Test, ROCF – Form A; Osterrieth, 1944), and explicit semantic memory (picture-naming task, verbal and visual semantic matching tasks from the GRECO neuropsychological semantic battery, BECS GRECO; Merck et al., 2011). The semantic battery assesses the integrity of the same 40 items (20 biological entities and 20 artifacts) in both verbal and visual input modalities (words and black-and-white drawings). Language skills (regular and irregular word reading; single-word repetition of the Boston Diagnostic Aphasia Examination, BDAE; Goodglass & Kaplan, 1972) and visuoperceptual performances were also assessed (copy condition of the ROCF – Form A; embedded figures subtest of the “Protocole d'Evaluation des Gnosies Visuelles”, PEGV; Agniel, Joannette, Doyon, & Duchéin, 1992; Benton Facial Recognition Test, BFRT; Benton et al., 1994).

All the patients exhibited normal performances on RCPM, which contrasted with their impaired overall DRS scores, as expected, given the well known vocabulary and comprehension deficit in SD. Furthermore, all the patients displayed an apparently spared day-to-day memory. Only one of them (SD2) scored below the normal range on one of the two episodic memory tasks. Regarding their performances on the explicit semantic assessment, they were all significantly impaired on picture naming. Six of them performed abnormally on both the verbal and visual semantic matching tasks, with only SD5 and SD7 exhibiting a deficit restricted to the verbal version of the task. Their overall level of semantic impairment on these explicit tasks was expressed under three labels: mild, moderate and severe (see Table 2). Finally, none of them displayed a deficit on language tasks that did not critically depend on semantic object knowledge (i.e., word repetition and regular word reading). One patient (SD7)'s performance was impaired on a visuoperceptual task (BFRT).

The neurological examination was normal for all eight SD patients. Neuroimaging (MRI scans) revealed atrophy predominantly in the temporal lobes. Atrophy was bilateral, but more pronounced on the left side in four patients (see Table 1). Three patients exhibited an almost left-sided temporal atrophy (SD4, SD7, and SD8) and one left-handed patient presented with right temporal atrophy (SD6). Seven patients also underwent ¹⁸fluorodeoxyglucose PET (FDG-PET) imaging, which revealed good topographical concordance between hypometabolism and areas of atrophy.

Only four of the patients (SD2, SD4, SD5 and SD6) underwent a follow-up assessment at one year. Indeed, one patient presented with such a dramatic decline in semantic abilities that she was no longer able to perform the task, another one deceased (by committing suicide) and the two remaining participants were not available to participate at follow up. The four patients were administered the same neuropsychological battery as before, including the experimental implicit lexical-decision priming task. The neuropsychological data at follow up essentially revealed a further small decline in overall DRS scores for three patients (SD2, SD4 and SD6). All four patients exhibited poorer performances on at least one of the three explicit semantic tasks. Their overall semantic impairment on these explicit tasks (i.e., mild, moderate and severe) yet remained at the same level as at the baseline (see Table 2).

2.1.2. Controls

Thirty-one healthy volunteers were recruited (see Table 1 for demographic data). All were native French speakers and had no history of neurological or psychiatric disorders, or drug or alcohol abuse. Prior to taking part, they all provided their written informed consent.

They were matched with the SD patients for age ($U=90$, $z=-1.186$, $p=0.249$), sex ($\chi^2(1)=0.315$, $p=0.575$) and years of education ($U=116.5$, $z=-0.265$, $p=0.798$).

All these control participants were included after undergoing a short screening assessment to rule out any overall cognitive impairment (all DRS scores were above the cut-off point) or lexical semantic disorder (all scores above the cut-offs on the BECS GRECO subtests: picture-naming task, mean=39.1 ± 1, range=37–40; verbal semantic matching task, mean=39.9 ± 0.5, range=38–40; visual semantic matching task, mean=39.9 ± 0.3, range=39–40; 6-item verbal semantic questionnaire, mean=237.4 ± 1.3, range=235–240) (see Table 2).

Table 2
Neuropsychological background data (highlighted scores: significantly below normal range).

Tests	Maximum score	Controls	SD patients											
			Baseline								Follow up			
			SD1	SD2	SD3	SD4	SD5	SD6	SD7	SD8	SD2	SD4	SD5	SD6
		Mean (standard deviation) or cut-off at 5%												
General cognitive functioning														
DRS	144	141 (2.2)	103	107	111	117	121	128	132	85	97	116	122	122
RCPM	36	15	33	35	33	34	36	33	26	33	34	31	32	33
Nonverbal episodic memory														
"La Ruche" visuospatial learning task														
Immediate free recall – sum of the 5 trials	50	16	–	–	38	47	32	36	40	39	–	45	47	45
Immediate forced-choice recognition	10	7	–	–	10	10	10	10	8	10	–	9	10	10
Delayed free recall	10	4	–	–	10	10	8	10	9	10	–	10	9	8
Delayed recall of ROCF – Form A	36	5	21	3	14	23	25.5	–	18.5	15.5	2	–	25.5	–
Working memory														
Digit span forward (WAIS-R)	9	4	6	5	6	6	4	7	6	6	6	6	4	7
Digit span backward (WAIS-R)	8	3	4	6	5	4	4	5	5	2	4	6	4	4
Language and semantic memory														
Irregular word reading test	18	17	14	16	12	18	11	17	17	14	14	17	15	17
Regular word reading test	18	17	18	18	17	18	18	18	18	17	18	18	18	18
Single word repetition subtest (BDAE)	10	9	10	10	9.5	10	10	10	10	10	10	10	10	10
BECS GRECO picture-naming task	40	39.1 (1)	0	2	3	10	14	13	21	1	1	5	10	6
BECS GRECO Verbal semantic matching task	40	39.9 (0.5)	24	25	17	25	31	36	35	20	21	25	28	32
BECS GRECO Visual semantic matching task	40	39.9 (0.3)	26	24	37	27	39	33	39	29	21	27	32	34
BECS GRECO – sum of the 3 tasks	120	118.9 (1)	50	51	57	62	84	82	95	50	43	57	70	72
Level of the overall semantic impairment (mild: 1; moderate: 2; severe: 3)			2	2	1	1	1	1	1	2	2	1	1	1
Visuo perceptual abilities														
Benton Facial Recognition Test	54	38	50	54	49	44	49	44	36	52	46	48	49	46
PEGV – Embedded figures subtest	36	30	36	36	35	36	36	36	35	36	36	36	36	36
Copy of ROCF –Form A	36	29	34	36	35	35	35	33	35	36	33	34	35	31

2.2. Experimental materials and design

2.2.1. Priming stimuli

In the implicit semantic priming task, the primes were the names of biological entities or artefacts, whereas the targets were features associated with the prime concepts. Targets could be either a proper noun or an adjective corresponding to a visual or contextual feature. In the visual condition, word pairs were selected so that the target referred to a visuo perceptual feature (color, shape, distinctive part) of the prime-object (e.g., "ostrich" priming "neck"). In the contextual condition, the target referred to an object currently associated with the prime in the environment (e.g., "bed" priming "pillow"). If all the visual word pairs and some contextual ones involve part-whole relationships, a substantial difference exists between these two sets of items. In the visual condition, word pairs share an inextricable part-whole link since one item is a component of the other, in an inseparable way (e.g., "ostrich-neck"; "cat-whiskers"; "broom-handle"). In contextual condition, items were separable, so that one item can exist independently from the other (e.g., "ring-diamond", "squirrel-hazelnut"; "envelope-stamp").

The targets were composed of one, two or three syllables (see Table in Supplementary material). The word pairs were associatively and semantically related and were selected from the data collected by Laisney et al. (see Laisney et al., 2011, for more methodological details). Briefly, these word pairs were generated by students ($N=129$) in two verbal association tasks. In these two tasks, the students had to produce the first word that came to mind in response to inductor words. We retained 44 semantically related prime-target pairs: 22 priming pairs with a visual attribute and 22 others with a contextual one. In each condition, half the items corresponded to living concepts and the other half to nonliving entities. Four subsets of priming pairs were thus constituted: (1) visual attributes for biological entities (e.g., "elephant" priming "tusk"); (2) visual ones for artifacts (e.g., "cap" priming "eyeshade"); (3) contextual attributes for biological entities (e.g., "squirrel" priming "hazelnut"); and (4) contextual ones for artifacts (e.g., "small boat" priming "oar"). We added 44 unrelated pairs (e.g., "jail" priming "stamp") to the 44 semantically related pairs (e.g., "envelope" priming "stamp"). We then added a further 60 filler pairs (e.g., "stone" priming "violin") to reduce the proportion of semantically related word pairs to below 30%. Our lexical-decision task also included 148 pairs where the prime was a word and the target a pseudoword (e.g., "night" priming "guilcha"). The pseudowords were constructed in accordance with the following rules: they were all pronounceable, and they all respected the orthographic structure of the French language. Like the target words, these pseudowords were composed of one, two or three syllables. The final version of our lexical-decision priming task therefore contained 296 pairs.

Each target (word or pseudoword) was presented twice in this monitoring task, while all the primes were encountered once, so that a target could never be linked to the same prime twice. The targets differed between the visual and the contextual conditions. In each attribute condition, the targets appeared once with a semantically related prime and again with an unrelated prime.

The targets of the four priming pairs subsets (visual attributes for biological entities, visual ones for artifacts, contextual attributes for biological entities, contextual ones for artifacts) were matched for lexical frequency (Lexique database; New, Pallier, Brysbaert, & Ferrand, 2004), one-way analysis of variance (ANOVA), $F(3, 43)=1.233$, $p=0.310$, for letter length, $F(3, 43)=0.733$, $p=0.539$, and for syllable number, $\chi^2(6)=4.32$, $p=0.633$. In both semantically related and unrelated conditions, the primes of these four subsets were also matched for lexical frequency (primes for the related condition, $F(3, 43)=2.066$, $p=0.120$; primes for the unrelated condition, $F(3, 43)=0.955$, $p=0.423$), for letter length (primes for the related condition, $F(3, 43)=2.101$, $p=0.115$; primes for the unrelated condition, $F(3, 43)=1.571$, $p=0.211$), and for syllable number (primes for the related condition, $\chi^2(6)=10.22$, $p=0.116$; primes for the unrelated condition, $\chi^2(6)=9.14$, $p=0.166$). We also compared these four subsets in terms of the strength of the verbal association between prime and target in the semantically related word pairs. The frequency with which a word was produced in response to an inductor in the verbal association task was taken as a measure of the strength of that verbal association (Laisney et al., 2011). Our four priming pairs subsets did not differ on this variable, $F(3, 43)=0.705$, $p=0.555$. Matching word pairs for this confounding variable is by far required since Moss, Ostrin, Tyler, and Marslen-Wilson (1995b) and Lucas (2000) emphasized that verbal association can lead to a "boost" in priming effect, above the effect of semantic relationships alone.

The 296 pairs were split into three blocks that were counterbalanced between participants. Within each block, no target appeared twice, and items were pseudo-randomized so that the block never began with a related pair and there was no sequence of three identical consecutive responses (positive or negative).

2.2.2. Priming procedure

The design of our lexical-decision priming task was derived from Giffard et al. (2001, 2002), Giffard, Desgranges, Kerrouche, Piolino, and Eustache (2003) and Laisney et al. (2011). Stimuli were presented using SuperLab Pro 4.5 software (Cedrus Corporation, San Pedro, CA, USA). Responses were produced and recorded using the RB-830 8-button response pad (Cedrus Corporation, San Pedro, CA, USA). Participants were instructed to answer with their dominant hand by pressing one of the two colored buttons (green button for "yes" and red button for "no").

Before the test, the participants underwent a practice session featuring 34 word pairs: four related pairs, 15 unrelated pairs and 15 word-pseudoword pairs.

Participants were asked to read each prime and target out loud, in order to train their ability to read primes displayed only briefly. This training session lasted until each participant was able to read each word and pseudoword easily and accurately.

Each lexical-decision trial began with a fixation cross that remained in the middle of the screen for 1000–1500 ms (duration randomized across trials). Next, a prime word was displayed for 200 ms, followed by a blank screen for 50 ms. The target then appeared and remained on the screen until a response was recorded. The stimulus onset asynchrony (SOA) was set at 250 ms. A short SOA is recommended to reduce the use of expectancy strategies (i.e., the use of a prime as a cue for generating possible target items related to the prime; Neely, 1977; Ober, 2002) and promote the involvement of automatic processes. There was a 1000 ms inter-stimulus interval between each trial.

Each block was separated by a short break lasting 5 min. At the beginning of each block, participants were instructed as follows: “You will be shown word pairs that you must read to yourself. For each word pair, you must determine whether or not the second word belongs to the French language. Press the green button for “yes, the letter string is a French word”, and the red button for “no, the letter string is not a French word”. You must respond as quickly as possible.” We focused the instructions on RT speed to optimize the intervention of automatic processes, even though a recent study (Stefaniak, Meulemans, & Willems, 2010) revealed a smaller impact of manipulating instructions (speed vs. accuracy) on the responses of older adults compared with younger ones, in an implicit lexical-decision task.

2.3. Statistical analysis

Statistical analyses were performed using SPSS Statistics 12.0 software (SPSS Inc., Chicago, IL, USA). Analyses were carried out first on *accuracy* (percentage of correct responses), then on RTs. In the RT analyses, we only considered correct responses and ruled out extreme outliers. Outliers were defined at an individual level and corresponded to any score more than three interquartile ranges (IQRs) from the rest of the scores (indicated by asterisks in the SPSS boxplot graphs).

We focused our analyses on *priming effect measures*. We therefore ran group (controls vs. SD patients) \times link (related vs. unrelated) \times attribute (visual vs. contextual) mixed-design ANOVAs on the raw data, with link and attribute as repeated measures and group as a between-participants factor. As planned comparisons, we used paired-samples *t*-tests to compare performances on related versus unrelated pairs for the two priming conditions taken together, then, separately for the visual and contextual attributes. We then compared the two groups' performances on every condition (related for visual, unrelated for visual, related for contextual, unrelated for contextual). Since each of the four priming pairs subsets was only composed of 11 items (i.e., visual attributes for biological entities, visual ones for artifacts, contextual attributes for biological entities and contextual ones for artifacts), the contrast between the priming effects obtained for those subsets should be considered with more caution. As subsidiary analyses, we thus performed a group (controls vs. SD patients) \times link (related vs. unrelated) \times attribute (visual vs. contextual) \times domain (living versus nonliving entities) ANOVA, as well as planned within-groups analyses to determine whether or not there is any effect of the domain of knowledge upon the priming results and to identify in which priming pairs subset a significant effect was mainly observed.

Thereafter, we ran a link (related vs. unrelated) \times attribute (visual vs. contextual) ANOVA on the raw RT data transformed into *priming percentages* (priming percentage = [mean RT for unrelated condition – mean RT for related condition] / mean RT for unrelated condition $\times 100$). We used the priming percentages – first proposed by Balota, Watson, Duchek, and Ferraro (1999), then recommended by Giffard et al. (2001, 2002) – to reduce any impact of cognitive slowing on the magnitude of the patients' priming effect.

Finally, we carried out intra-individual analyses on the follow-up data for the four SD participants (SD2, SD4, SD5 and SD6). These analyses helped us to determine the number of patients who displayed a dissociation between the two attribute conditions, at the two assessment times. For this purpose, we employed the Bayesian criterion for dissociations in case studies, associated with the Bayesian standardized difference test (BSDT) developed by Crawford, Garthwaite, and Porter (2010). This programme allowed us to identify a “strong dissociation” (i.e., meeting the following criteria: the standardized difference between the individual's scores in the X and Y conditions of a task must be significant, as must a deficit in at least one of the two conditions). This statistical method was applied to performances (RTs only) at baseline and at one-year follow up for each of the four SD patients.

For the overall analyses, all tests were two-tailed and the statistical level of significance was set at $p=0.05$.

3. Results

3.1. Semantic priming effect at baseline

3.1.1. Accuracy

A group \times link \times attribute ANOVA on the percentage of correct responses only showed a main effect of group, $F(1, 37)=18.432$,

$p<0.001$, in that the SD patients were less accurate than controls (see Table 3). No main effect was observed for either link, $F(1, 37)=0.068$, $p=0.795$, or attribute, $F(1, 37)=1.724$, $p=0.197$. Neither the group \times link, $F(1, 37)=0.068$, $p=0.795$, nor the link \times attribute, $F(1, 37)=0.745$, $p=0.394$, interaction reached significance. The group \times attribute interaction tended towards significance, $F(1, 37)=3.776$, $p=0.06$. Planned comparisons revealed no significant differences explaining this trend towards significance (see Table 3). Otherwise, the group \times link \times attribute interaction was not significant, $F(1, 37)=1.252$, $p=0.270$.

Finally, neither controls nor SD participants' accuracy differed across priming conditions (visual related vs. contextual related, for controls: $t(30)=1.680$, $p=0.103$; for SD patients: $t(7)=-0.768$, $p=0.468$). Besides, we failed to show any difference in accuracy between the two domains of knowledge (living vs. nonliving entities) in both controls and SD patients (Controls, related condition: $t(30)=1.680$, $p=0.103$, unrelated condition: $t(30)=0.571$, $p=0.572$; SD patients, related condition: $t(7)=-0.001$, $p=1$, unrelated condition: $t(7)=-1.656$, $p=0.142$).

3.1.2. Reaction times (RTs)

A group \times link \times attribute ANOVA indicated significant main effects of group, $F(1, 37)=58.198$, $p<0.001$, $\eta^2_{\text{partial}}=0.611$, link, $F(1, 37)=7.139$, $p=0.011$, $\eta^2_{\text{partial}}=0.162$, and attribute, $F(1, 37)=12.823$, $p=0.001$, $\eta^2_{\text{partial}}=0.257$. The link \times attribute interaction reached significance, $F(1, 37)=17.631$, $p<0.001$, $\eta^2_{\text{partial}}=0.323$, unlike the group \times link, $F(1, 37)=0.041$, $p=0.840$, and group \times attribute, $F(1, 37)=0.242$, $p=0.626$, interactions. The group \times link \times attribute interaction was significant, $F(1, 37)=32.190$, $p<0.001$, $\eta^2_{\text{partial}}=0.465$.

Planned within groups comparisons indicated a significant overall priming effect for controls (i.e., when both kinds of attributes were collapsed), with shorter mean RTs in the related condition than in the unrelated one (related condition: mean = 625.4 \pm 89.2; unrelated condition: mean = 644.8 \pm 88.4; $t(30)=-3.664$, $p<0.001$), but no such overall priming effect for the SD patients (related condition: mean = 1050.6 \pm 282.1; unrelated condition: mean = 1076.4 \pm 264.7; $t(7)=-1.121$, $p=0.299$). Furthermore, when each attribute condition was considered separately, we found contrasting results for the SD group compared with controls (see Table 3). For controls, a significant priming effect was revealed for visual attributes (unrelated vs. related pairs, $t(30)=-4.705$, $p<0.001$) and no priming effect for contextual ones (unrelated vs. related pairs, $t(30)=-1.143$, $p=0.262$). These contrasted performances could not be explained by any differential level of complexity between the two attribute priming conditions (for controls: visual related vs. contextual related conditions, $t(30)=1.881$, $p=0.07$). As contrasted with the controls' pattern of performances, the SD participants exhibited an absence of priming in the visual condition (unrelated vs. related, $t(7)=1.105$, $p=0.306$), but a significant priming effect in the contextual one (unrelated vs. related, $t(7)=-6.771$, $p<0.001$). For each planned comparison (related for visual, unrelated for visual, related for contextual, unrelated for contextual), controls responded significantly faster than the SD participants, even after the Bonferroni correction for multiple comparisons (all $ps\leq 0.001$).

As subsidiary analysis, we performed a group \times link \times attribute \times domain ANOVA which confirmed and replicated the previous results and showed significant main effects of group, link, attribute and domain (all $ps<0.01$). Besides, this analysis indicated no significant group \times attribute \times domain interaction, $F(1, 37)=1.140$, $p=0.293$, while group \times link \times domain interaction tended towards significance $F(1, 37)=3.776$, $p=0.06$, and link \times attribute \times domain interaction reached significance, $F(1, 37)=15.891$, $p<0.001$, $\eta^2_{\text{partial}}=0.300$. Finally, the group \times link \times attribute \times domain interaction was significant, $F(1, 37)=12.968$, $p=0.001$,

Table 3
SD patients' and controls' mean accuracy (expressed as percentage of correct responses) and mean RTs in milliseconds (standard deviations: SD) for both semantically related and unrelated word pairs in the two attribute conditions (visual and contextual). *p*: *p* values for the paired-samples *t*-tests.

		Visual			Contextual		
		Related condition mean (SD)	Unrelated condition mean (SD)	<i>p</i>	Related condition mean (SD)	Unrelated condition mean (SD)	<i>p</i>
Accuracy	Controls	99.6 (1.4)	99.1 (2.2)	0.375	99 (2.5)	98.8 (2.3)	0.786
	SD patients	89.8 (13.3)	90.9 (11.9)	0.685	93.2 (9.1)	92 (9.9)	0.649
RTs	Controls	632 (88.8)	662.9 (101.7)	< 0.001	618.6 (93.2)	626.8 (78.7)	0.262
	SD patients	1107.1 (307.7)	1054 (263.7)	0.306	998.6 (266.2)	1097.2 (271.1)	< 0.001

$\eta^2_{\text{partial}}=0.260$. In the control group, planned comparisons yielded a significant priming effect in the visual condition for both biological and artifacts concepts (biological, unrelated vs. related, $t(30)=-2.380$, $p=0.024$; artifacts, unrelated vs. related, $t(30)=-4.495$, $p<0.001$), but no priming effect in the contextual one, regardless the domain of knowledge (biological, unrelated vs. related, $t(30)=-0.651$, $p=0.520$; artifacts, unrelated vs. related, $t(30)=-1.257$, $p=0.219$). In the SD group, the same analyses revealed a significant priming effect in the contextual condition for only living entities (biological, unrelated vs. related, $t(7)=-2.619$, $p=0.034$; artifacts, unrelated vs. related, $t(7)=-1.436$, $p=0.194$). In the visual condition, an unexpected trend towards significance was observed for living entities, in that RTs for related pairs tended to be longer than for unrelated ones (biological, related pairs mean = 1137.7 ± 345.5 , unrelated pairs, mean = 993.5 ± 231.9 , $t(7)=2.187$, $p=0.065$; artifacts, unrelated vs. related, $t(7)=-1.293$, $p=0.237$).

3.1.3. Priming percentages for RTs

A group \times attribute ANOVA failed to reveal a significant main effect of group, $F(1, 37)=0.157$, $p=0.694$, but the attribute effect, $F(1, 37)=11.074$, $p=0.002$, $\eta^2_{\text{partial}}=0.230$, was significant. The group \times attribute interaction was significant, $F(1, 37)=25.376$, $p<0.001$, $\eta^2_{\text{partial}}=0.407$. Planned comparisons revealed contrasting patterns of performances between the SD patients and controls, with higher priming percentages for the SD patients than for controls in the contextual condition ($U=24$, $z=-3.478$, $p<0.001$), and lower percentages in the visual one ($U=67$, $z=-1.982$, $p=0.048$) (see Fig. 1).

3.2. Semantic priming effect at follow up

One year later, we administered the same experimental priming task to SD2, SD4, SD5 and SD6 again. Only two of these four SD patients had initially exhibited a significantly strong dissociation between the priming effects for the two attributes (SD2: BSDT, $Z\text{-DCC}=-7.699$, $p<0.0001$, and SD5: BSDT, $Z\text{-DCC}=-6.861$, $p<0.0001$; compared with SD4: BSDT, $Z\text{-DCC}=0.606$, $p=0.556$, and SD6: BSDT, $Z\text{-DCC}=-1.871$, $p=0.072$). However, all four patients displayed a strong dissociation one-year later (SD2: BSDT, $Z\text{-DCC}=-5.433$, $p<0.0001$; SD4: BSDT, $Z\text{-DCC}=-3.966$, $p<0.001$; SD5: BSDT, $Z\text{-DCC}=-2.266$, $p=0.038$; SD6: BSDT, $Z\text{-DCC}=-2.336$, $p=0.028$).

SD2, SD4 and SD5 exhibited an absence of priming in the visual condition, but a significant priming effect in the contextual condition. Only SD6 exhibited a significantly increased priming effect for the contextual attributes, contrasting with a slightly lower (but still within the normal range) effect for the visual ones.

It is worth noting that there is no clear link between the overall level of semantic impairment (i.e., performances on the three

explicit semantic tasks) and the presence or the absence of a strong dissociation between the priming effects in the two attribute conditions.

Taken together, we can briefly sum up these results as follows: the SD patients generally displayed the opposite pattern of performances to controls when analyses focused on the two attribute conditions. The SD group showed no priming for visual attributes, but a significant priming effect for contextual ones. Furthermore, the follow-up data provided evidence of the robustness of the dissociation between priming performances in the two attribute conditions. This dissociation persisted between baseline and follow up, and the number of patients exhibiting this strong dissociation increased from two SD patients at baseline to four at one-year follow up.

4. Discussion

This study was designed to explore the integrity of two types of features: visuoperceptual versus contextual/functional. More specifically, we sought to verify the robustness of previous findings (i.e., the preservation of functional features vs. the impairment of perceptual ones) by restricting the features included under the functional heading to contextual ones only. A second goal was to determine whether this hypothetical differential deterioration in perceptual versus functional attributes remained significant as the disease progressed, which is why we assessed four of the patients at one-year follow up.

At a group level, we failed to find an overall priming effect (i.e., when both kinds of features were collapsed) for the SD patients, unlike controls. The absence of an overall priming effect in the SD patients was in line with previous findings (Nakamura et al., 2000; Rogers & Friedman, 2008). However, when we considered the two types of semantic features separately, we observed contrasting patterns of performances for the SD patients and controls. The latter displayed significant priming in the visual condition and no priming effect in the contextual one, whereas the SD participants exhibited an absence of priming for visual features, but significant priming for contextual ones. We also found evidence for the robustness of this effect in the SD patients. Intra-individual analyses indicated that the dissociation (i.e., no priming effect for visual attributes and a significant priming effect for contextual ones) remained significant between baseline and follow up. Moreover, the number of patients exhibiting a strong dissociation also increased between these two assessment times, since all four SD patients met the Bayesian criterion for strong dissociation at one-year follow up. These results are in accordance with Tyler and Moss' core findings (Moss et al., 1995a; Tyler & Moss, 1998). Through the use of semantic priming paradigms, these authors were able to determine that functional attributes are preserved for longer than category relations (Moss et al., 1995a; Tyler & Moss, 1998) and perceptual attributes (Moss

et al., 1995a). Their longitudinal study (Tyler & Moss, 1998) also emphasized that functional properties are more resistant to brain damage. Although we sought to bypass the potential methodological shortcomings identified in these studies (i.e., the inclusion of extremely heterogeneous features under the functional heading), by restricting functional features to a contextual subtype, we obtained identical findings. We also observed a deterioration in visuo-perceptual features (i.e., absence of the priming effect in this condition) at an early stage in the disease. This agreement between previous findings and our results suggests that impairment of visuo-perceptual features, as opposed to contextual-functional attributes, is a key deficit in SD. The status of the latter is still uncertain and raises further issues.

We claim *first of all* that the priming effect for contextual attributes is the result of semantic change in SD patients, rather than an artifact arising simply from cognitive slowing, as was previously proposed by Nebes, Brady, and Huff (1989). According to these authors, the probability of exhibiting shorter RTs than controls for semantically related pairs is higher when patients display longer RTs for unrelated pairs. This argument was advanced mainly to disprove the hyperpriming effect reported in AD using lexical-decision priming tasks (Chertkow et al., 1989). Hyperpriming was thus regarded as an artifact resulting from general cognitive slowing. In our study, as expected, we also found a slowing of lexical-semantic processing in our SD group, as their RTs for unrelated pairs were longer than those of controls. Nevertheless, our main finding remained significant even when analyses were carried out on priming percentages, which tend to correct the priming effect by taking account of RTs for unrelated pairs.

Second, we consider that our results mainly reflect genuine semantic mechanisms rather than the intervention of nonsemantic lexical processes. The involvement of lexical processes is known to enhance the priming effect (Lucas, 2000; Moss et al., 1995b), and Rogers and Friedman (2008) reported significant and normal priming effects in their SD group in a lexical associative condition. More recently, Perri, Zannino, Caltagirone, and Carlesimo (2011) argued that studies using verbal association tasks to select their semantically related word pairs cannot rule out an intervention of lexical processes in their priming effects. Although our items were also chosen from two verbal association tasks, we believe that any minimal lexical intervention processes could not account for the priming pattern observed in the SD patients, as we had taken the methodological precaution of matching the four priming pair

subsets on the strength of verbal association. Our main finding can thus be interpreted in terms of semantic mechanisms resulting in differential patterns of performances in controls and the SD group.

Third, we argue that the priming effect observed in the SD patients in the contextual condition can be regarded as a sign of a semantic knowledge disequilibrium, rather than over-spaced contextual features. As proposed by Perri et al. (2011), a priming effect that is observed in patients without any significant corresponding effect in controls presumably reflects semantic deterioration (cf. previous interpretations of hyperpriming effects). Arguments in favor of a semantic deficit underlying the abnormally increased priming effect in patients were first put forward by Chertkow et al.'s (1989) in AD. Giffard and colleagues (2001, 2002) also reported hyperpriming in the category-coordinate condition in AD patients, interpreting it as a reflection of semantic deterioration. They hypothesized that an abnormally increased priming effect stems from a decline in the specific semantic features that are needed to discriminate between close exemplars of the same semantic category (e.g., “tiger” – “lion”). As the “tiger lost its stripes” and the “lion, its mane”, the remaining, spared features were shared by both entities and entirely overlapped, leading to confusion between the two concepts. These assumptions were put forward to explain an abnormal “positive” priming effect as a sign of semantic deficit. However, they do not hold here. The hypothesis of abnormally increased priming effects stemming from a deterioration in specific attributes was essentially developed for concepts sharing coordinate relationships. It is far more difficult to apply to contextual attributes where two concepts (e.g., “squirrel” – “hazelnut”) share only a contextual relationship and no other obvious common features.

Alternatively, we speculate that the priming effect observed in the contextual condition in our SD patients was indicative of a profound semantic disequilibrium altering the relationship between two distinct and parallel semantic systems. To explain this assumption, we should first specify that contextual attributes are also known as “thematic” relations, referring to complementary roles between two entities. Complementary-based relations can be defined as the frequent co-occurrence of two entities in events or situations, and refer to the link between concepts that occur together in time and space (Denney, 1975). Thematic, or complementary-based, relations are currently contrasted with similarity-based relations, also called “taxonomic” relations. These two systems refer to different relationships between concepts (Lin & Murphy, 2001): the thematic system addresses the external relations between two entities, whilst the taxonomic system refers to the concepts' internal structure and, more specifically, to the categories' features. Preferential recruitment of one or other of the systems has previously been demonstrated in childhood, from a developmental perspective. Nguen and Murphy (2003) thus reported a preference for thematic rather than taxonomic categorization in children. Students have also been found to prefer thematic relationships, when required to choose between these two types of categorization (Lin & Murphy, 2001). These two systems have also been reported to coexist in healthy adults. Nevertheless, many studies have yielded more conflicting results. Kalénine et al. (2009) demonstrated an advantage of taxonomic over thematic relationships regarding both RTs and accuracy on a matching task, while Sachs, Weis, Krings, Huber, and Kircher (2008a) failed to highlight any difference between thematic and taxonomic conditions on these two measures in a forced-choice category construction task. Contrasted results were also highlighted in studies using implicit lexical-decision priming tasks. Exploring the specific role of each cerebral hemisphere in semantic processing, visual-half-field behavioral priming studies reported greater priming effect for thematic than taxonomic

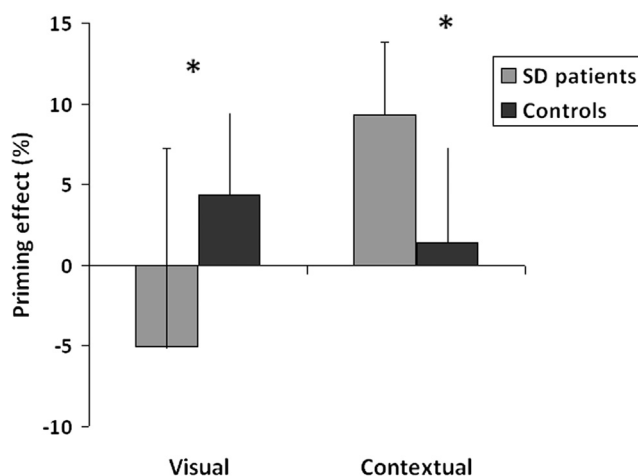


Fig. 1. Priming effect expressed as a percentage [(mean RT for unrelated condition – mean RT for related condition)/mean RT for unrelated condition *100] in the visual and contextual conditions for the SD patients and controls. *Significant between-group comparisons at $p < 0.05$. Error bars represent standard error of the mean.

relationships and also that taxonomic priming effect occurred for longer SOAs (Abernethy & Coney, 1993; Bouaffre & Faita-Ainseba, 2007). These results are in line with fMRI studies investigating the neural correlates of semantic priming for taxonomic and thematic relationships. Indeed, Kotz, Cappa, von Cramon, and Friederici (2002) demonstrated that healthy adults took longer to respond to taxonomic relations than to thematic ones. More recently, Sachs et al. (2008b) found a larger priming effect in the thematic condition than in the taxonomic one, together with more errors for taxonomic relationships. Sass, Sachs, Krach, and Kircher's (2009) priming study reported clearer results in favor of thematic processes in healthy adults, as they only found a significant priming effect in the thematic condition, and none for taxonomic relationships. By contrast, Jones and Golonka (2012) failed to replicate these previous findings of differential priming effects for thematic and taxonomic relationships. There are three possible explanations for these overall conflicting results in healthy adults. First, they could stem from interindividual variability (Mirman & Graziano, 2012a; Simmons & Estes, 2008), in that each participant may differ in the weighting allocated to taxonomic and thematic semantic processing. Second, they may arise from the knowledge domain to which the experimental items belong. Both Sachs et al. (2008a, 2008b) and Sass et al. (2009) used paradigms in which the words depicted solely nonliving objects, whereas Kalénine et al. (2009) compared biological concepts with artifacts. Moreover, Kalénine et al. (2009) demonstrated a significant interaction between knowledge domain and type of semantic relationship, in that taxonomic relationships were identified more quickly for living entities, and thematic relationships were recognized faster for nonliving ones. Third, Jones and Golonka (2012) interpreted the advantage of thematic over taxonomic relationships in previous priming studies as the consequence of integrative relationships within the thematic word pairs set. The fact that thematic word pairs shared mixed (both thematic and integrative) relationships could potentially explain the greater priming effect observed in that condition compared with the taxonomic one. In their work, Jones and Golonka (2012) isolated integrative relationships as a third kind of semantic relations, distinct from thematic and taxonomic ones. They referred to Estes and Jones (2009)'s study to define the integrative relationships as a link between two concepts which can be easily brought together to create a unitary representation. Integrative relationships include the internal component (e.g., “cherry” – “pit”; “fruit” – “cake”) and external component (e.g., “tricycle” – “pedals”; “siren – ambulance”). Nevertheless, the authors admitted that integrative and thematic relations are not exclusive and may overlap. In the present study, that kind of semantic relationship is present in our contextual word pairs set (e.g., “oak tree” – “acorn”) as well as in our visual one (e.g., “bicycle” – “handlebar”). These additional integrative relationships could exert a possible influence on the priming effects in both conditions. Such an influence cannot therefore be retained as a probable confounding factor explaining our core finding (i.e., the significant priming in the visual condition but not in the contextual one for controls and the reverse pattern of performances in the SD group).

We rather believe that our findings can be interpreted in terms of the differential recruitment of one of these two coexisting systems. This interpretation holds good even though our priming paradigm did not directly contrast taxonomic versus thematic relations, but rather visuo-perceptual versus contextual-functional features. Perceptual features have been shown to be a core determinant of similarity-based/taxonomic relationships (Medin & Ortony, 1989), whereas complementary-based/thematic processing relies mainly on contextual ones. Davidoff and Roberson (2004) were the first to suggest an overlap between perceptual and taxonomic categorization abilities. In a case study, these

authors described an aphasic patient (symptoms close to Wernicke's aphasia: LEW) with impairment of both taxonomic and perceptual categorization, contrasting with preserved thematic categorization. Evidence for crucial links between perceptual features and taxonomic relationships has also been forthcoming in fMRI studies. Taxonomic relationships appear to activate neural bases that are commonly reported when perceptual processing is engaged (i.e., visual associated areas, bilaterally), whereas thematic relationships recruit a bilateral temporoparietal network (Kalénine et al., 2009). It is worth noting that the involvement of the temporoparietal junction – known to be involved in motion, action and spatial processing – has been consistently revealed across several studies (De Zubizaray, Hansen, & McMahon, 2013; Mirman & Graziano, 2012b; Schwartz et al., 2011). Concerning the neural correlates of semantic priming for taxonomic and thematic relationships in implicit lexical-decision tasks, several fMRI studies (Kotz et al., 2002; Sachs et al., 2008b; Sass et al., 2009) revealed that taxonomic relationships require the recruitment of additional areas in the right hemisphere, interpreted as reflecting a more effortful semantic processing than for thematic one. Contrasted to thematic relationships, taxonomic processing resulted in enhanced activations in cuneus (Kotz et al., 2002) – in accordance with Kalénine et al. (2009) – precuneus (Kotz et al., 2002; Sachs et al., 2008b) and isthmus of cingulate gyrus (Kotz et al., 2002) and was interpreted as relying on perceptual processing, episodic memory retrieval and on detection of semantic relations. In Sass et al. (2009), a direct comparison between the two semantic relationships revealed an activation in the left superior temporal sulcus for thematic over taxonomic conditions, due to an opposite level of responses in this area. While thematic processing induced response-enhancement in the left superior temporal sulcus, response-suppression was observed in taxonomic condition. Partially distinct neural basis and differential patterns of neural responses between the two semantic relationships were also highlighted by Sachs et al. (2011). These authors observed response-suppression in the right middle frontal gyrus for the taxonomic processing, whereas thematic relationships resulted in response-enhancement in the left inferior frontal gyrus. Sachs et al. (2011) recalled that the right middle frontal gyrus is associated with mental search within the semantic network, higher retrieval effort and decision uncertainty, so that the response-suppression could be the sign of priming effect as taxonomic processing depends upon perceptual/similarity-based relationships. The left inferior frontal gyrus is involved in executive control of retrieval and selection from the semantic memory, so that the response-enhancement for thematic processing could reflect the spread of activation between connected nodes. Finally, a direct contrast between the two semantic relationships revealed an increased activation for taxonomic relationships in the right insula lobe – known to be involved in working memory and attentional components – while the same area tended to decrease in the thematic condition.

These last results regarding the opposite patterns of response-enhancement and suppression in identical areas between the thematic processing and the taxonomic one could raise the issue of partial reverse neural processing underlying thematic and taxonomic relationships. Furthermore, some authors suggested that those two distinct and parallel systems coexist but also compete in healthy adults (Maguire, Brier, & Ferree, 2010). In their work using event-related spectral perturbation analyses, they demonstrated that theta power increased over right frontal areas for thematic relationships and that alpha power increased over parietal areas for taxonomic ones. They proposed that this increased alpha power may be the consequence of the inhibition of thematic relationships, to give way to taxonomic processing.

Regarding the results of our semantic priming paradigm, we can infer that in controls, similarity-based/taxonomic relationships were automatically advantaged over complementary-based/thematic relationships, leading to a significant priming effect for visuo-perceptual features and no priming for contextual–functional ones. In the SD patients, the deterioration of visuo-perceptual attributes impeded the similarity-based/taxonomic processes and thus brought complementary-based/thematic relationships to the fore. Such an interpretation is not at variance with previous studies assessing thematic relationships by means of explicit semantic matching tasks (e.g., the Pyramids & Palm Trees Test; Howard & Patterson, 1992) and demonstrating that SD patients performed below normal range (Bozeat et al., 2000; Jefferies & Lambon Ralph, 2006). Note that in the present study, SD participants exhibited a lower level of performances than controls on both accuracy and RTs in the contextual condition, suggesting that their thematic relationships knowledge is not spared. Nonetheless, that impairment is not discordant with our hypothesis that SD patients rely more upon the complementary-based/thematic relationships system (even impaired) than on the similarity-based/taxonomic one.

Additionally, our line of interpretation was strengthened by subsidiary results in the SD group when complementary analyses were focused on the two subsets of living priming pairs. A significant priming effect was reported in the contextual condition for the biological entities while an unexpected trend towards significance was observed in the visual condition for biological entities, in that their RTs for related pairs tended to be longer than for unrelated pairs. That tendency to slowly treat prime pairs might be considered as an extinction of the link between a concept and its visual attribute. We speculated this line of interpretation from the Laisney et al. (2011)'s schematic evolution (and involution) of semantic priming effects in relation to semantic memory deterioration. These authors proposed that the priming effects in the distinctive (e.g., “zebra” priming “stripes”) and in the shared (e.g., “duck” priming “feather”) feature conditions progressively and dramatically fall under the normal mean at severe levels of semantic deterioration, until a possible negative priming effect might occur. This negative priming effect could thus be considered as a sign of a distressing semantic breakdown, so that a feature could no longer be associated to a concept. We propose to interpret these subsidiary results as partially fitting with the predictions developed in the sensory/functional theory (SFT; Warrington & Shallice, 1984). According to this model, perceptual features would be more salient for biological entities and critical to identify exemplars of living concepts. The SD patients' results were in agreement with the SFT account since the impact of perceptual attributes impairment appeared to be more pronounced for biological concepts. At the same time, it is worth noting that the SD patients yielded a significant priming effect in the contextual condition only for biological concepts. We could thus consider that the state of semantic disequilibrium essentially affects knowledge about living entities. Since the ability to identify perceptual similarities between concepts was previously reported to be a core determinant to taxonomic relationships (Davidoff & Roberson, 2004) and since the two semantic relations systems were demonstrated to coexist and compete, we argue that these subsidiary results reinforce our hypothesis that breakdown of visuo-perceptual attributes may disrupt similarity-based/taxonomic relations and give way to complementary-based/thematic ones. Nonetheless, even if these subsidiary analyses could partially fit with the SFT, this is not supported by the main results of the direct analysis contrasting living versus nonliving entities in the SD group. These last results therefore clearly contradict the core assumption of this model. Indeed, in line with prior SD cases (AN, CS, MA, AT, SL, IW; Lambon Ralph, Howard, Nightingale, & Ellis, 1998; Lambon Ralph

et al., 2003; MF: Barbarotto, Capitani, Spinnler, & Trivelli, 1995; see also case review by Capitani, Laiacina, Mahon, & Caramazza, 2003), we demonstrated that impairment of visuo-perceptual features in SD was not related to any global difference in accuracy between the two domains of knowledge (living vs. nonliving entities), yet expected by the SFT predictions.

One limitation of our main line of interpretation concerns the difference in the nature of the prime and the target in the two attribute conditions. One could argue that visual condition involves a concept–feature link whereas contextual one refers to a concept–concept link. More generally, that criticism could be addressed against many experimental designs built in line with the SFT. Indeed, Tyler and Moss (1998) confronted in the same design perceptual features: “crocodile–green” versus functional ones “crocodile–river”. Nonetheless, boundaries between a concept and a feature or an attribute remain unclear. We acknowledge that this may be a matter of debate. However, according to Wong and Gallate (2012), we assume that any feature – even if it is a single color – can be seen as a unit of meaning and as a concept in itself.

Our results suggesting that impairment of visuo-perceptual features is a key deficit in SD could run counter to several reports demonstrating that semantic deficit in SD was not confined to concepts mainly depend upon visuo-perceptual information, by means of explicit semantic tasks. Indeed, significant difference between the two domains of living and nonliving knowledge was rarely reported in SD patients (Lambon Ralph et al., 2003; Lambon Ralph, Lowe, & Rogers, 2007) and studies assessing the concreteness effect in SD highlighted an advantage of concrete/high imageability words over abstract/low imageability ones (Hoffman, Jones, & Lambon Ralph, 2013; Hoffman & Lambon Ralph, 2011; Jefferies, Patterson, Jones, & Lambon Ralph, 2009). These findings were interpreted in light of the “hub and spoke” semantic framework (Lambon Ralph, Sage, Jones, & Mayberry, 2010; Patterson et al., 2007; Rogers et al., 2004). This theory states that the anterior temporal lobe (ATL) is a critical region for a single convergence zone (a “hub”) that brings together various modality-specific information from different sensory, motor and linguistic regions (the “spokes”) into an amodal and coherent representation. Since SD is characterized by a bilateral atrophy and hypometabolism maximal in the ATLs (Mummery et al., 2000; Nestor, Fryer, & Hodges, 2006), the “hub and spoke” theory predicts the absence of any category-specific semantic deficit and any differential feature impairment after ATL lesions. Our finding of a more severe impairment for visuo-perceptual features could at first sight dismiss that strong prediction of the model. Nevertheless, such a more pronounced deficit for visuo-perceptual attributes in SD patients was also highlighted, to some extent, by Hoffman, Jones, and Lambon Ralph (2012). In SD, these authors showed no advantage for items rich in visual information, contrary to items rich in other sensory-motor information, and interpreted it as a sign of a later additional breakdown of a modality-specific spoke region (specialized in the visual information processing), in line with a graded hub-and-spoke model of conceptual knowledge (i.e., a gradual convergence of information along the temporal lobes, with visual information in the posterior areas giving way to pan-modal representations in the ATLs). Two arguments could strengthen that conception. Firstly, visuo-perceptual features, whenever tested through similarity-based/taxonomic relationships, were shown to activate more posterior areas rather than ATLs (Kalénine et al., 2009; Kotz et al., 2002). Secondly, the hypothesis of a later additional breakdown of a modality-specific spoke region specialized in the visual information processing seems to be in agreement with our results at follow up, since more patients exhibited an absence of priming in the visual condition one year later. That graded hub-and-spoke framework could be helpful to explain the visuo-perceptual features impairment exhibited by the SD patients. Nonetheless, given that our study focused on the cognitive organization rather than on the neural basis of semantic knowledge in SD, we

could not accurately rely upon neuroanatomical accounts such as the hub and spoke model to interpret our core findings. Rather, the distinction proposed between thematic and taxonomic systems based on experimental psychology as a main factor organizing semantic knowledge at a cognitive level perfectly fits with our concerns i.e., with the fact SD patients generally displayed the opposite pattern of priming performances to controls.

To conclude, our priming paradigm comparing two semantic features (visuoperceptual versus contextual–functional attributes) revealed a reverse pattern of performances in the SD patients compared with controls. While controls exhibited priming in the visual condition but no significant priming effect in the contextual one, the SD patients showed exactly the opposite performances. We argue that these priming effects were not an artifact caused by cognitive slowing in the SD patients, and that they reflected semantic mechanisms rather than lexical processes. We interpreted the reverse pattern of performances in terms of a semantic knowledge disequilibrium and, more specifically, in terms of the differential recruitment of one of the two coexisting and competing systems of semantic relationships. In controls, the similarity-based/taxonomic relationships were automatically advantaged over complementary-based/thematic relationships, leading to a significant priming effect for visuoperceptual features without any priming for contextual–functional ones. In the SD patients, as perceptual features were impaired, the system of thematic relationships had to take over from the similarity-based/taxonomic one.

These results need to be set against the relative independence of SD patients in activities of daily living, despite their massive semantic deficit (Bier & Macoir, 2010; Bier et al., 2013). This relative independence is quite astonishing, given that in other degenerative diseases (including AD), functional disorders hamper everyday life at a far earlier stage in the pathology. Regarding their functional abilities, SD patients have long been described with preserved object use despite their semantic memory breakdown (Buxbaum, Schwartz, & Carew, 1997; Hodges et al., 2000; Lauro-Grotto, Piccini, & Shallice, 1997). Hodges et al. (2000) and Bozeat, Lambon Ralph, Patterson, and Hodges (2002) isolated several factors explaining the spared abilities to use objects: the residual conceptual knowledge, the conceptual familiarity, the personal familiarity and the visual object affordances (i.e., mechanisms that support object use directly from visual and/or tactile input). Nevertheless, Negri, Lunardelli, Reverberi, Gigli, and Rumiat (2007) argued that semantic knowledge is not a key factor in the success of object use. They proposed that these abilities depend upon motor knowledge, which may be represented separately from semantic knowledge in the brain. A possible alternative factor might be considered regarding the spared abilities to use objects and further investigations are needed to determine whether thematic relationships can operate as a relay system capable of managing knowledge about the use and function of concepts. Lin and Murphy (2001) related thematic categories to the concept developed by Barsalou (1991) of “goal-derived categories”, where entities are brought together in a schema-like organization and share mutual constraints. We therefore need to determine whether knowledge of the context in which an object frequently appears, and its associations in space and time with other entities, is enough to deduce its scope of use.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2013.11.024>.

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