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Role of the anterior temporal lobe in repetition and semantic priming: evidence from a patient with a category-specific deficit

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Abstract

Neuroimaging studies in healthy participants have implicated anterior temporal lobe regions and the fusiform gyrus in repetition priming and semantic priming. Only the investigation of patients with selective lesions, however, can establish the necessity of these particular regions. To this end, we administered three tests of repetition priming (pseudoword identification; masked-form priming; category-exemplar generation) and a test of semantic priming to a patient (J.P.) with a category-specific deficit stemming from bilateral damage to the anterior fusiform gyrus and anterior temporal regions. On all of the repetition priming tasks, J.P. showed priming effects within 1 S.D. of 10 age- and education-matched CON; ANOVAs indicated no interaction between group and prime condition. These findings suggest that the anterior fusiform and anterior temporal lobe are not required for these priming effects. J.P. also showed normal repetition priming even for items that he had never been able to name or to provide semantic information about. On the semantic priming task, J.P. showed normal levels of priming across categories. When we separately analyzed his priming for items he could never name or access information about versus items that he had been able to name on at least two testing sessions, we found priming for the latter items, but not for the former. This result suggests that category-specific deficits resulting from damage to the anterior temporal lobes may disrupt the automatic, rapid access of semantic information of some items.

Keywords: Perceptual priming; Conceptual priming; Semantic priming; Temporal lobectomy; Category-specific deficit

1. Introduction

Memory is dissociable into multiple components. One distinction is between declarative (explicit) and non-declarative (implicit) memory. Declarative memory refers to processes requiring conscious or intentional retrieval of information. Non-declarative memory, in contrast, demonstrates the effect of prior experiences on performance using tasks that do not require conscious information retrieval. Priming encompasses non-declarative memory tasks that measure response bias or reduction in response latency resulting from prior exposure to identical or related information.

Priming is not monolithic, and a number of distinct types of priming have been suggested. Repetition priming is one subdivision, whereby prior exposure to a stimulus facilitates or biases a response to a perceptually or conceptually identical stimulus. Semantic priming is another subset whereby exposure to a stimulus facilitates or biases response to a conceptually related (but not identical) stimulus.

2. Neural substrates supporting repetition priming

Even within these subtypes, dissociable processing mechanisms may underlie the priming effects. For example, repetition priming may be separated into perceptual and conceptual domains [28,29].

2.1. Perceptual repetition priming

Perceptual repetition priming refers to the facilitated processing of an object or word due to its repetition. In the standard paradigm, participants study a list of objects or words, and after a brief delay, perform what is presented as an unrelated task (e.g. identifying words flashed very briefly on

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the screen). Priming is measured as the reduction in latency to identify previously presented as compared to unstudied words.

Perceptual priming appears to occur at a pre-semantic and pre-lexical level: priming can occur for newly formed representations (e.g. pseudowords) that have no pre-existing representations [19,29,55]. In addition, levels of processing manipulations do not alter the magnitude of the priming effect [55]. Instead, the effect is modulated by perceptual overlap at study and test: the effect is greatest when the perceptual characteristics, such as font, size, and format, remain constant [26,54,74].

Neuroimaging studies that have examined the neural substrate of perceptual repetition priming in healthy adults have frequently found priming-related decreases in activation in a variety of cortical regions. Reductions in activation have been discovered in visual areas including extrastriate occipital cortex [6,7,45,52] and posterior fusiform regions [6,7]. Decreases in activation (for studied as compared to unstudied items), also frequently extend into more anterior regions of the inferior temporal cortex [6,7,75] and insular cortex ([7,48]; see [5,53] for review). These data suggest that repetition priming may result in reduced neural activity in these regions.

Neuroimaging studies of normal control participants, however, cannot establish the necessity of brain regions [47] because the areas activated by a particular task represent the functional network correlated with a cognitive operation, and may include components that are not required for task performance. Investigations of patients with focal lesions, in contrast, can pinpoint the anatomical regions whose integrity is necessary for task performance.

Within the domain of perceptual repetition priming, multiple studies in patients have indicated that posterior temporal-occipital regions are needed for successful performance. Patients with damage to these posterior regions do not show perceptual repetition priming effects [9,17,30]. Only a few lesion studies, however, have examined whether the more anterior regions that also show modulation in neuroimaging experiments are required for successful performance. Some of these studies have suggested a role of the anterior temporal lobe in item repetition effects: patients with anterior temporal lobectomies show reduced ERP repetition effects during explicit recognition tasks (e.g. patients show similar ERP responses to “old” and “new” words [49,60,65]), suggesting altered responses to item repetition. Other research examining performance on implicit measures of item repetition, however, has pointed to preserved perceptual repetition priming in patients with damage to the anterior temporal lobes. Srinivas et al. [62] found that a patient with bilateral anterior temporal lobe damage, resulting from semantic dementia, showed normal levels of perceptual priming for novel and familiar objects. Geva et al. [20] also found preserved perceptual priming (for proper names) in a patient with prosopanomia and damage to the left temporal lobe.

The first goal of the present study was to examine perceptual repetition priming for novel verbal material in a patient (J.P.) who had bilateral lesions of the anterior portion of the temporal lobes. We asked whether the effects of repetition of verbal material would be present with anterior temporal lobe damage, thus allowing leverage on the question of whether the anterior temporal regions implicated in neuroimaging studies are critical for successful perceptual repetition priming.

2.2. *Conceptual repetition priming*

The second goal of this study was to examine the necessity of the anterior temporal lobes for conceptual repetition priming. Support for a conceptual basis of repetition priming comes from studies of cross-modal and masked-form repetition priming: for example, hearing a word will later facilitate a response to the visually presented word [31], or seeing a masked word prime can decrease naming latency for a picture [14]. These priming effects cannot rely on perceptual similarity, because the study and test phases (or prime and target elements) use different formats.

Neuropsychological data also support the dissociation of perceptual and conceptual priming. Alzheimer’s disease results in impaired performance on conceptual priming tasks, such as category-exemplar generation [70] or word-stem completion priming [8,18,23], but preserved performance on perceptually based repetition priming tasks using pseudowords [28,29] or novel visual stimuli [18]. Conversely, damage to the temporo-occipital region impairs repetition priming for pseudowords [29], but not for conceptual tasks [30].

The neuroimaging studies that have addressed the neural substrates of conceptual priming have found priming-related changes in temporal regions including the middle and superior temporal gyri [1,52], as well as (relatively posterior) inferior temporal regions [7,59]. The literature examining the effect of temporal lobe damage on conceptual repetition priming is sparse. Nielsen-Bohlman et al. [43] found that patients with unilateral inferior temporo-occipital lesions were impaired on word-stem completion priming tasks, which are believed to rely on perceptual and conceptual features [17–46]. These patients’ lesions were located more posteriorly than that of J.P. To our knowledge, no studies have assessed conceptual repetition priming in patients with bilateral damage to the anterior portion of the temporal lobes. This issue was, therefore, the second goal of the present study.

3. Are category-specific semantic deficits accompanied by implicit conceptual knowledge?

Conceptual repetition priming and semantic priming are impaired in patients with degenerative diseases that cause widespread damage to the semantic knowledge system.

Alzheimer's disease patients are impaired on conceptual priming tests, including category-exemplar generation [70] and word-stem completion [8,18,23,28], as well as on semantic priming tasks [4]. Similarly, patients with semantic dementia frequently show impaired performance on semantic priming tasks [39,40,42,69]. Although the temporal lobe damage in these diseases is relatively diffuse, neuroimaging studies suggest that the anterior temporal lobes may be particularly important for the priming effects: there appear to be priming-related activation decreases in left inferior prefrontal cortex and left anterior temporal cortex [32,41]. To our knowledge, no study has investigated semantic priming in a non-demented patient with a relatively circumscribed lesion in the anterior temporal lobes. We, therefore, sought to determine whether J.P. would show normal levels of semantic priming.

As a corollary of this goal, we wanted to examine whether J.P. would show different priming effects for spared and impaired categories, on tasks of conceptual repetition as well as semantic priming. We found no studies that systematically examined this issue in non-demented patients with category-specific semantic deficits (but see [56,72] for relevant discussion). One study [39] examined semantic priming in a patient with advanced semantic dementia who had a deficit primarily for non-living objects, that patient showed impaired semantic priming (also see [3] for a similar study in Alzheimer's disease patients). It is an open question as to whether such findings generalize to patients with restricted category-specific deficits in the absence of dementia. We were interested in examining whether a patient with a stable, category-specific deficit on tasks requiring naming or explicit generation of semantic knowledge would show category-specific impairments on implicit memory tasks that rely on rapid and automatic processes.

4. Present experiment

To investigate whether repetition and semantic priming were intact following an anterior temporal lobe lesion, we administered three tests of repetition priming (pseudoword identification, masked-form priming, and category-exemplar generation) and one test of semantic priming to J.P. and control participants. Within the domains of conceptual repetition priming and semantic priming, we wanted to discover whether J.P.'s priming capacities would differ for categories on which he showed preserved semantic processing as compared to categories on which he was impaired. While it is clear that J.P.'s declarative semantic knowledge is impaired for select categories of information, this investigation sought evidence about whether his deficit extended to automatic, implicit processes. We, therefore, analyzed J.P.'s priming with words from spared and impaired categories. We believe that this study is the first to examine, in a non-demented patient, whether category-specific naming deficits extend to tasks that require automatic, fast-access to information, or whether the deficits are confined to tasks that require declarative, intentional access of information (see [3,39,69] for similar studies in demented patients).

5. Methods

5.1. Participants (patient J.P.)

At the time of testing, J.P. was a 27-year-old, right-handed college graduate. His cognitive abilities were normal apart from a stable category-specific deficit.

5.1.1. Case history

In September 1995, at age 22, J.P. was admitted to the Berkshire Medical Center, Pittsfield, MA, with a 2-week history of severe nausea, vomiting, and diarrhea. A CT scan revealed a left temporal lobe lesion. MRI confirmed the left-hemisphere damage and showed right-hemisphere abnormality as well. J.P. was diagnosed with herpes simplex encephalitis and started on treatment with Acyclovir. Despite treatment, his condition worsened, and he became increasingly confused and lethargic. A CT scan revealed hemorrhage in the left anterior temporal lobe with uncal herniation. Due to the progression of the herniation, a left temporal lobectomy with resection of the hematoma was performed. He improved gradually following the surgery and was discharged from the hospital in October 1995. In June 1997, he was sufficiently improved to return to college. Only the naming impairment remained a concern. In June 1999, J.P. graduated from college, and he began work as an engineer, the following month.

5.1.2. Neuroanatomical lesion

An MRI scan performed in 1999 using a 3 Tesla Signa System scanner revealed the left anterior temporal lobe lesion as well as right-hemisphere signal abnormality (Fig. 1). Sulcal widening and enlargement of the right temporal horn indicated shrinkage of the right anterior temporal lobe. Bilateral signal abnormality was seen in the fusiform gyrus and in the white matter lateral to the temporal horn. The posterior third of the inferior temporal and fusiform gyri were spared bilaterally.

5.1.3. Category-specific semantic deficit

J.P.'s category-specific deficit has been tracked from 1996 to 2001. His performance has been stable over that time, and he has been consistently impaired on the categories: fruits, vegetables, birds, insects, and musical instruments. In contrast, his performance on other categories has been relatively preserved.

J.P. was tested on the same picture naming task [61] in 1996, 1997, and 1999. On all three occasions, he was impaired on the categories of fruits (1996—20%, 1997—50%, 1999—50%), vegetables (1996—25%, 1997—50%, 1999—50%), birds (1996—37.5%, 1997—62.5%, 1999—50%),

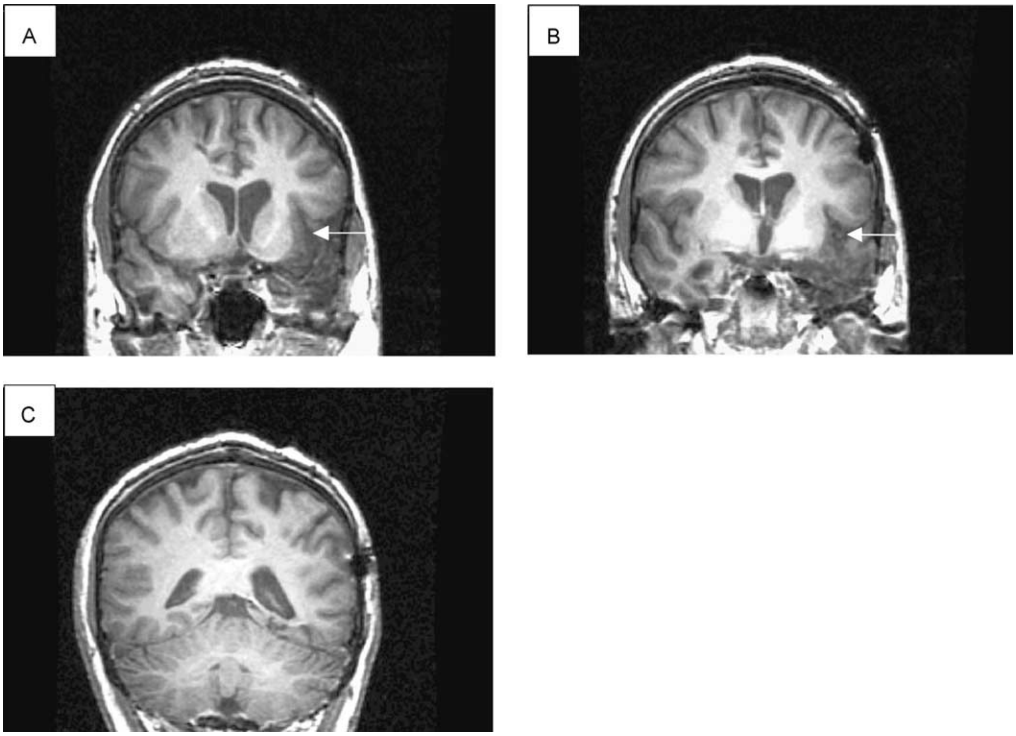

Fig. 1. Location of J.P.'s lesion. In the left-hemisphere, J.P.'s lesion included the entire temporal pole (the area of resection; see arrows in A and B) and extended to the anterior third of the superior temporal gyrus. The middle temporal gyrus appeared damaged in its anterior half (A, B). The left lateral ventricle was larger than the right (A, B, C). Signal abnormality was seen in the anterior fusiform gyrus bilaterally (B); the posterior third of the anterior fusiform gyrus was spared (C).

insects (1996—62.5%, 1997—75%, 1999—62.5%), and musical instruments (1996—37.5%, 1997—50%, 1999—37.5%). He also showed a deficit in the domain of flowers (10%), on a different set of pictures (from Lorraine Tyler, personal communication). In contrast, he showed relatively normal performance for the categories of animals (1996—75%, 1997—100%, 1999—100%), clothing (1996—87.5%, 1997—87.5%, 1999—100%), vehicles (1996—100%, 1997—100%, 1999—100%), and parts of the human body (1996—100%, 1997—100%, 1999—100%). This pattern of spared and impaired performance remained when items were matched for familiarity and visual complexity [58].

In 2001, J.P. was tested with a different set of pictures [11] and again was found to be impaired on the categories of fruits and vegetables (34%), birds (45%), flowers (8%), and musical instruments (36%). Insects were not included on this task. His naming ability was relatively preserved for animals (81%), clothing (92%), furniture (93%), vehicles (80%), and parts of the human body (100%). J.P. also showed stability not only in the categories in which he is impaired, but also with the particular items. A χ^2-test of association indicated a consistency between the first and second testing sessions that exceeded that expected by chance ($\chi^2 = 7.54$, $P < 0.05$), and also between the second and third sessions ($\chi^2 = 11.49$, $P < 0.001$).

J.P.'s deficit extends to accessing semantic information. He is impaired at identifying the real-life colors of black-and-white line drawings from impaired categories (e.g. he said that a pumpkin was purple) but not from spared categories. This deficit existed when he was asked to name the color of the objects, and when he was asked to pick out the color of yarn that would best match the color of an object. J.P. also showed deficits in matching an object to its definition, for the above-mentioned categories (fruit—25%; vegetable—37.5%; birds—75%; insects—75%; instruments—75%) but not for spared categories (all 100%). He also scored below normal on tasks requiring him to answer questions regarding the functional and visual properties of fruits and vegetables (<75%, only these two categories were assessed on this task). More details on his category-specific deficit are reported in [56].

5.1.4. *General cognitive function*

In testing sessions conducted between 1997 and 2000, we assessed J.P.'s overall cognitive function. We report here the relevant scores on tests of visual ability, attention, frontal lobe function, memory, and I.Q. More details are reported in [58].

5.1.5. *Visual acuity*

J.P.'s visual acuity and depth perception were normal as assessed by: Snellen Acuity Test, Randot Stereo Acuity Test (Stereo Optical, Chicago, IL), and the Vistech Contrast Sensitivity Test (Vistech Consultant, Dayton, OH). He also

Table 1
J.P.'s scores on the Wechsler Adult Intelligence Scale (A) and Wechsler Memory Scale (B) as a function of testing session

	October 1995	February 1996	April 1996	June 1997	August 2000
A					
Full scale I.Q.	91	107	113	121	116
Verbal I.Q.	86	94	96	102	106
Performance I.Q.	100	125	135	140	128
	April 1996	June 1997	July 1999	August 2000	
B					
General memory	84	92	88	104	
Verbal memory	73	88	76	96	
Visual memory	128	101	133	122	
Attention and concentration	105	110	110	95	
Delayed memory	86	107	83	111	

completed four tests of color vision without errors (City University Color Vision Test [16]; Ishihara Test for color blindness [25]; Farnsworth Dichotomous Test for color blindness [13]; and Lanthony Color Test [33]).

His score on the Benton Facial Recognition Test [34] was normal compared to that of 20 age- and education-matched CON (J.P.'s score = 45, CON mean = 47.76, S.D. = 3.57), as were his scores on the Hidden Figures Test [67] (25/27 correct for Part I, 7/7 for Part II, 6/7 for Part III, and 10/10 for both Parts IV and V, all within the time limits). His copy of the Rey-Osterrieth Complex Figures Test [44] was perfect.

A neuro-ophthalmological examination in July 1999 revealed a modest refractive error in the left eye, correctable with pinhole to better than 20/20. Acuity in the right eye was better than 20/20. The only possible abnormality was detected in the right homonymous superior quadrant of the visual field. According to the neuro-ophthalmological report, this deficit "was subtle ... and should not be disruptive for any visual tests." A neurological examination was normal.

5.1.6. Attention and frontal lobe function

J.P. performed normally on tests of frontal lobe function, including the Stroop Test [64] (109 words, 74 color, 58 color/words, means for 20 age- and education-matched CON = 112.2, 79.3, 48.7) and Wisconsin Card Sorting Test [22,38] (6 categories, 10 total errors, no perseverative errors). His forward digit span was 8 and his backward digit span was 7.

5.1.7. Memory

J.P.'s scores on the Wechsler Memory Scale and Wechsler Adult Intelligence Scale [73] are reported in Table 1. His 1 h recall of the Rey-Osterrieth Complex Figures Test [44] was normal (23/36, 20 age- and education-matched CON = 23.9, S.D. = 3.42). On the Recognition Memory Test [71], J.P. showed normal memory for faces (44/50) but impaired recognition for words (36/50). His poor performance on this task is due, at least in part, to the inclusion of words from impaired categories.

5.1.8. Healthy control participants

J.P.'s performance was compared to that of 10 age-, education- and sex-matched control participants (CON). They were MIT undergraduate or graduate students whom we screened to eliminate those with a history of alcoholism, major heart disease, cancer, or neurological or psychiatric disorders. All participants were right-handed native English speakers. They were tested individually and were remunerated at a rate of US$ 10 per hour for their participation.

5.2. Tasks

5.2.1. Repetition priming

5.2.1.1. Pseudoword repetition priming (adapted from [30]). The studied stimuli were 38 six-letter pseudowords (consonant-vowel-consonant-consonant-vowel-consonant). Participants first were shown each pseudoword for 2000 ms and were asked to pronounce it as it appeared on the computer screen.[1] They were asked to be consistent in their pronunciation of the pseudowords, but not to worry about whether their pronunciation was "correct." They saw 16 pseudowords presented once and 16 pseudowords presented three times (once within each third of the list). Because repetition priming effects can be small, and because we were comparing the priming effects of a single patient to a group of CON, we wanted to assure that the magnitude of priming in the CON was sufficient to allow comparison with that of J.P. We, therefore, used item repetition because this manipulation has been shown to increase the size of

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[1] This task deviates from the method used in some perceptual priming tasks in that there are both visual-perceptual (study-test presentation) and auditory (participants' pronunciation) components. Nonetheless, this task has been used to measure priming of perceptual identification in numerous studies comparing performance of patients with Alzheimer's disease [29], bilateral occipital lobe lesions [30], and medial temporal lobe lesions [30]. The reliability of this task has been measured in a large group of healthy participants; priming effects elicited by the task show sensitivity to perceptual manipulations just as do other perceptual priming tasks [28].

the priming effect [27,30]. Three filler pseudowords were presented at the beginning and end of the list to remove primacy and recency effects.

This study phase was followed by a perceptual identification task. Participants were told that they would perform a task unrelated to the study task. They were instructed that a series of "nonsense words" would appear briefly on the computer screen and that they were to identify each of the words by pronouncing them aloud. Each trial was preceded by a fixation cross ("+") in the middle of the screen. Participants were asked to fixate on that cross in preparation for the appearance of the pseudoword. On each trial, a pseudoword was then flashed on the computer screen and replaced by a backward mask ("######") which remained on the screen for 250 ms. In this way, participants were shown 64 pseudowords (16 had been presented once in the study list; 16 had been presented three times; and 32 had not been studied). These pseudowords were initially presented for 20 ms. If the pseudoword was not identified correctly, it was presented in another trial at a longer duration (30 ms). Additional increments of 10 ms were used until the participant could correctly pronounce each of the pseudowords. The dependent measure was the stimulus exposure duration at which participants correctly identified pseudowords: a priming effect would be indicated by a significant reduction in the exposure time necessary to identify studied as compared to unstudied words.

5.2.1.2. Category-exemplar generation priming (adapted from [30,36]). On day 1, participants completed a category fluency task with eight categories: for each category, they were asked to generate as many category-exemplars as possible in 60 s. This measure established a fluency baseline. On day 2, participants first studied a list of low-typicality exemplars from eight categories (e.g. "papaya"; [2]). This list included five exemplars from each of the eight categories (presented in random order), as well as four filler items at the beginning and end of the list. Participants were asked to indicate whether each object was natural or man-made. We chose this task because priming is greater following semantic as compared to non-semantic processing of words at study [63]. After a brief delay, and in what was presented as an unrelated task, participants were asked to generate as many exemplars as possible in 60 s, from a category whose exemplars comprised the prior study (e.g. "fruit"). Priming was measured as the increased proportion of target exemplars generated within the first eight items in the primed condition relative to the baseline condition. We selected four categories (flowers, fruits, vegetables, instruments) from those in which J.P. showed impairment in naming and accessing semantic information, and four categories (weather, parts of the human body, clothing, animals) in which J.P. showed normal performance. Priming effects were calculated for (a) all categories, (b) impaired categories, and (c) spared categories.

5.2.1.3. Masked-form repetition priming (adapted from [14]). Participants viewed 52 black-and-white line drawings of common objects [61] on a computer screen. On half of the trials, a word prime that was identical to the picture name (e.g. *chair*—CHAIR) preceded the picture. On the other half of the trials, the word prime was unrelated to the target picture name, but began with the same phoneme (e.g. *check*—CHAIR). Each unrelated prime was a word of the same length as the corresponding target. Words were presented in uppercase, black letters; pictures were presented as black-on-white drawings.

Each trial consisted first of a forward pattern mask, presented for 500 ms. Participants were asked to fixate in the middle of the mask. The mask was immediately followed by the presentation of the prime word, for 25 ms. This prime word was then immediately followed by the presentation of a backward mask (15 ms). The presentation of the target picture immediately followed this mask. The picture stayed on the screen until participants responded, and a voice-activated response time was measured. The next trial sequence followed a 3 s delay.

There were a total of 52 trials. On 26 trials, the word named the picture; on 24 trials, the word was semantically unrelated to the picture. Half of the pictures (distributed equally across the related and unrelated prime conditions) were items for which J.P. showed preserved naming and semantic access (taken from the categories of body parts, clothing, animals), and half were items for which J.P. showed impaired naming and semantic access (taken from the categories of fruit, instruments, vegetables). We defined items as impaired if J.P. had been unable to name or to give semantic information about the item in at least three testing sessions conducted over a 4-year span. We considered items to be spared if J.P. had never made an error in naming or in giving semantic information about the item in testing sessions spanning the 4-year period. Spared and impaired items were matched for word length and number of syllables.

No mention was made of the existence of a word prime, and consistent with the results of Ferrand et al. [14], participants appeared to have little consciously accessible information about the prime. J.P. and seven CON were unaware that a word had been presented, and the remaining three CON indicated that they believed a "letter string" had been presented, but were unsure whether it was a real word, and indicated that they could not read the word.

Priming was measured as the facilitation in naming time for items preceded by their name as compared to items preceded by a semantically unrelated word. We analyzed this priming effect separately for (a) all items, (b) spared items, and (c) impaired items.

5.2.2. Semantic priming

5.2.2.1. Lexical decision priming (adapted from [35]). The stimuli were based on category-exemplar word pairs [2]. Participants were given 140 trials. On each trial, there was first a row of three asterisks (∗∗∗) presented for 200 ms; then, a blank screen was presented for 200 ms; following the blank screen was a 140 ms warning tone, followed again by a blank screen for 200 ms. The prime word was then presented for 400 ms, and after a 50 ms delay, the target stimulus was presented. Participants were asked to make a lexical decision about the target word by pressing a button labeled "W" for word or "N" for non-word; response time was recorded. On 120 trials, participants were shown a category word (e.g. "fruit") followed by a target word that was either a category-exemplar (e.g. "apple"), an unrelated word (e.g. "robin"), or a pseudoword. Of the 120 target words, 40% were exemplars of the prime; 30% were unrelated to the prime; and 30% were pseudowords. On 20 trials, the word "blank" appeared rather than a category word. We kept the relatedness proportion low, because a low proportion of semantically related trials reduces the likelihood that participants' performance reflects attentional, rather than automatic, processes [66,68]. Participants were asked to make a lexical decision about the target word by pressing the letter "W" for word or "N" for non-word. Priming effects were measured as the difference in reaction time between trials with a category-exemplar target versus an unrelated target word.

We selected items for which J.P. showed impaired naming and semantic access (taken from the categories of fruits and musical instruments), and items for which J.P. showed normal performance (from the categories of animals and clothing). For impaired categories, unrelated target words were also items for which J.P. showed impaired naming; for spared categories, unrelated target words were items on which his performance was preserved. As in the masked-form priming task, impaired items were defined as those that he had been unable to name or generate semantic information about in at least three testing sessions. Spared items were those that he had always been able to name. Items used in spared and impaired categories were matched for word length and number of syllables. Related and unrelated words were matched for frequency. Items used in this task were different from those used in the cross-form repetition priming study or the category-exemplar generation study. Priming effects were computed for (a) all categories, (b) impaired categories, and (c) spared categories.

5.3. *Data analysis*

We considered J.P. to be impaired when he performed 2 S.D. or more below the CON mean. We could not perform conventional parametric significance tests (*t*-tests or ANOVAs) across participants because these tests require within-group variances that cannot be obtained with a one-subject design (as with J.P.). We did, however, perform paired *t*-tests across items to look at the difference between the mean reaction times and scores of the two groups (J.P. and CON). All *P*-values reported are two-tailed. We also conducted repeated-measures ANOVA across items with item type (primed versus unprimed; spared versus impaired) as a between-item factor, and group (J.P. or CON) as a within-item factor.

6. Results

6.1. *Perceptual repetition priming*

6.1.1. *Pseudoword repetition priming*

We were interested in examining the effect of study exposure on the time needed to identify pseudowords. To this end, we conducted ANOVAs across items separately for CON and for J.P., with study exposure (studied, unstudied) as a within-items factor. These ANOVAs indicated that CON showed a significant effect of prior study ($F = 16.5$, $P < 0.001$) as did J.P. ($F = 5.3$, $P < 0.05$). We then examined whether the magnitude of this priming effect was similar in J.P. and CON by conducting an ANOVA across items with study exposure as a within-items factor and group (CON, J.P.) as a between-items factor. This ANOVA indicated a significant effect of prior study ($F = 16.3$, $P < 0.001$) but no effect of group and no group X study exposure interaction ($P > 0.2$). Subsequent *t*-tests indicated that J.P. ($t = 3.6$, $P < 0.01$) and CON ($t = 3.5$, $P < 0.01$) were faster to identify studied than unstudied words (Table 2).

We also examined the effect of study repetitions (one, three) on time to identify pseudowords. We first conducted ANOVAs across items separately for CON and J.P., with repetition as a within-items factor. These ANOVAs indicated that CON showed a significant effect of study repetition ($F = 13.2$, $P < 0.001$) as did J.P. ($F = 9.6$, $P < 0.001$). To examine whether the magnitude of the priming effect was similar in J.P. and CON, we conducted an ANOVA with repetition as a within-items factor and group as a between-items factor. The ANOVA found a significant effect of study repetitions ($F = 8.8$, $P < 0.01$) but no effect of group and no group X study repetition interaction.

We also looked at J.P.'s rank among the CON, based on the percentage difference of priming shown, e.g. (RT studied − RT unstudied)/RT studied. We divided by the RT to studied words to account for occasions on which J.P. performed more slowly (for studied and unstudied items) than CON. J.P. performed within 1 S.D. of the CON mean for words studied once, three times, and for unstudied words. He showed facilitated identification of studied versus unstudied words equal to or greater than five CON, and he showed a magnitude of speeded identification based on study

Table 2
Perceptual identification: time to identify words (in ms), as a function of number of prior exposures and group

	Mean identification time in ms (S.D.)		
	0 Exposures	1 Exposure	3 Exposures
CON	34.2 (7.0)	31.9 (8.9)	23.2 (4.4)
J.P.	40.6	28.1	23.4

repetitions greater than that of three CON. These rankings support the conclusion that J.P. showed a normal magnitude of perceptual priming with pseudowords.

6.2. Conceptual repetition priming

6.2.1. Masked-form repetition priming

To examine whether J.P. and CON showed significant priming, we conducted ANOVAs on the naming times for pictures with word condition (related, unrelated) as a within-items factor. CON showed a significant effect of word condition ($F = 72.1$, $P < 0.001$) as did J.P. ($F = 17.2$, $P < 0.01$). To determine whether the magnitude of the priming effect was equivalent in J.P. and CON, an ANOVA was conducted with word condition as a within-items factor, and group as a between-items factor. This ANOVA indicated a marginal effect of group ($F = 3.15$, $P < 0.10$) and a significant effect of word condition ($F = 24.7$, $P < 0.01$), but no group X word condition interaction. The group effect was due to the fact that J.P. was slower than CON at naming pictures preceded by either their correct name or a semantically unrelated word ($t = 2.69$, $P < 0.01$). His reaction times deviated by more than 2 S.D. from the CON mean. The lack of a group × word condition interaction suggests that while J.P. was slower overall, he showed similar cross-form repetition priming effects to CON (Table 3).

We also ranked J.P.'s priming performance among that of CON. J.P. showed facilitation levels greater than those of four CON. This result further supports the conclusion that J.P. showed normal cross-form repetition priming.

6.2.2. Comparison of impaired and preserved categories

When items were divided into categories in which J.P. showed preserved or impaired naming capacities, for spared categories, his reaction times were within 1 S.D. of the CON mean, and he did not differ significantly from the CON mean ($P > 0.10$; see Table 4). He was, however, slower for impaired categories ($t = 2.1$, $P < 0.05$), and he was equally slow (as compared to CON) when the target picture was preceded by its lexical label or an unrelated word (ANOVA indicated no category type X prime condition interaction; $P > 0.10$). Paired t-tests indicated that his priming effects did not differ significantly from CON for either spared or impaired categories ($P > 0.10$).

Repeated-measures ANOVA with category type (spared, impaired) and item type (primed, unprimed) as between-items factors, and group as a within-items factor, were conducted to look at the effect of J.P.'s category-specific deficit on priming. The ANOVA showed no effect of category type or group, and a marginal interaction of group and category type (J.P. was slower for impaired than spared categories; $F = 3.5$, $P < 0.10$), but there were no other significant interactions. Critically, there were no interactions between group, category type, and prime type. These results indicate that J.P.'s priming effects are equivalent to those of CON, and do not differ between spared and impaired categories. For spared and impaired categories, the magnitude of J.P.'s priming effects were within 1 S.D. of the CON mean. For spared categories, he showed priming greater than five CON, and for impaired categories he showed priming greater than six CON. These rankings, therefore, also support the conclusion that J.P. showed normal priming effects for spared and impaired categories of items.

We were also interested in whether there would be any effect on performance for always-impaired items (ones J.P. had never named or generated semantic information for, over a span of 5 years) as compared to usually-impaired items (ones J.P. had named in one or two testing sessions). We, therefore, conducted an ANOVA across items, with level of impairment (always-impaired, usually-impaired) and prime condition (primed, unprimed) as within-items factors. An ANOVA indicated no effect of impairment, a significant effect of prime condition ($F = 17.0$, $P < 0.05$), and no impairment X prime condition interaction. We hasten to add that due to the small sample size, we had little power to detect an interaction; nonetheless, these results provide suggestive evidence that J.P. showed priming for items on which he was always-impaired, as well as on items for which he was usually-impaired. The similar magnitude of the priming effects for always-impaired and sometimes impaired items support this conclusion (Table 5).

Table 3
Time to name pictures (in ms), as a function of prime type and group

	Mean identification time in ms (S.D.)		
	Semantically unrelated	Correct word	Facilitation
J.P.	1505	1360	145
CON	1073 (135)	975 (96)	98 (58)

Table 4
Time to name pictures (in ms), as a function of prime type and item type

	Mean identification time in ms (S.D.)		
	Unrelated word	Related word	Facilitation
Spared items			
J.P.	1122	1014	108
CON	1089 (180)	1019 (132)	70 (49)
Impaired items			
J.P.	1889	1686	203
CON	1103 (162)	967 (133)	136 (74)

Table 5
Time for J.P. to name pictures (in ms), as a function of prime type and consistency of impairment

	Mean identification time in ms (between-item S.D.)		
	Unrelated word	Related word	Facilitation
Always-impaired	1504 (401)	1235 (308)	269 (64)
Usually-impaired	1383 (351)	1146 (102)	236 (52)

Table 6
Percentage of first eight words generated that were target words, as a function of study condition and group

	Number of words	
	Unstudied	Studied
J.P.	0	6.25
CON	0.47 (0.76)	5.16 (2.09)

6.2.3. *Category-exemplar priming*

To examine whether J.P. and CON showed priming based on prior study of category-exemplars, we conducted ANOVAs separately for J.P. and CON with prime condition (primed, unprimed) as a within-items factor. These ANOVAs indicated that CON showed a significant effect of prime condition ($F = 7.0$, $P < 0.05$), as did J.P. ($F = 18.1$, $P < 0.01$). We then conducted an ANOVA with prime condition as a within-items factor, and group (CON, J.P.) as a between-items factor, to examine whether the magnitude of priming was similar in J.P. and CON. This ANOVA indicated a significant effect of prime condition ($F = 17.6$, $P < 0.001$), but no effect of group or group X prime condition interaction. These results suggest that J.P. showed a similar level of category-exemplar priming as did CON (Table 6).

We also ranked J.P.'s performance among CON. J.P. performed within 1 S.D. of the CON mean, and his level of priming was equal to or greater than that of all but one CON. This ranking supports the conclusion that J.P. showed normal conceptual[2] priming on this task.

6.2.4. *Comparison of spared and impaired categories*

Paired *t*-tests conducted across items showed that J.P. and CON demonstrated similar category-exemplar priming effects for spared and impaired categories ($P > 0.10$) (Table 7). The ANOVAs conducted separately for spared and impaired categories indicated an effect of prime condition (for spared categories, $F = 5.8$, $P < 0.05$; for impaired categories, $F = 8.1$, $P < 0.05$) but no effect of group or interaction between group and prime condition. Subsequent *t*-tests indicated no difference in the magnitude of the priming effect for J.P. and CON for spared categories or impaired categories ($P > 0.3$). We could not analyze always-impaired versus usually-impaired items because, due to the low typicality exemplars used in this experiment, J.P.'s performance on these items had not been assessed on multiple testing sessions. For spared and impaired categories, J.P. performed within 1 S.D. of the CON mean. Rankings placed his priming effects above those of three CON for spared categories, and six CON for impaired categories, further suggesting that J.P.'s priming effects were normal for spared and impaired categories.

Table 7
Percentage of first eight words generated that were target words, as a function of study condition, category type, and group

	Mean percentage generated	
	Unstudied	Studied
Spared categories		
J.P.	0	6.25
CON	0.31 (0.98)	3.44 (3.11)
Impaired categories		
J.P.	0	6.25
CON	0.63 (1.3)	6.9 (4.8)

6.3. *Semantic priming tasks*

6.3.1. *Lexical decision priming*

To examine whether J.P. and CON showed priming on this task, we first conducted ANOVAs across items separately for the two groups, with prime condition (primed, unprimed) as a within-items factor. These analyses indicated that CON showed a significant effect of priming condition ($F = 4.79$, $P < 0.05$) as did J.P. ($F = 3.86$, $P < 0.05$). To examine whether J.P. showed a similar magnitude of priming as CON, we conducted an ANOVA with group (J.P., CON) as a between-items factor. This analysis revealed a significant effect of group ($F = 12.05$, $P < 0.01$; J.P. was slower than CON), an effect of prime condition ($F = 4.26$, $P < 0.05$), and no interaction between group and prime condition. Subsequent *t*-tests also indicated no difference in the magnitude of priming effects between J.P. and CON ($P > 0.20$).

To further clarify whether J.P. showed similar priming to CON, we examined his ranking among CON. J.P. performed within 1 S.D. of the CON mean for all categories; he showed a magnitude of priming equal to or greater than six of the CON. These results support the conclusion that J.P. showed normal lexical decision priming.

6.3.2. *Comparison of impaired and preserved categories*

To investigate whether J.P.'s level of priming was different for spared and impaired categories, we conducted an ANOVA with category type (spared, impaired) and prime condition (primed, unprimed) as within-items factors, and group (J.P., CON) as between-items factors. This analysis indicated an effect of group ($F = 12.0$, $P < 0.01$; J.P. slower than CON) and prime condition ($F = 26.2$, $P < 0.001$), no effect of category type, and no significant interactions. We also conducted an ANOVA to examine how the category type (spared, impaired) affected the magnitude of the priming effect in J.P. and CON. This ANOVA indicated no effect of group or category type, and no group by category type interaction on the magnitude of the priming effect (Table 8). These results suggest that J.P. showed normal lexical decision priming for items on which he showed impaired naming and semantic access, as well as for items on which he showed normal performance.

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[2] We did not include a levels-of-processing manipulation in this task; we, therefore, cannot rule out contributions of perceptual priming to performance on this task.

Table 8
Time for J.P. and CON to make a lexical decision (in ms), as a function of prime type and item type

	Mean identification time in ms (S.D.)		
	Unrelated category	Related category	Facilitation
Spared items			
J.P.	672	602	70
CON	630 (65)	563 (50)	67 (32)
Impaired items			
J.P.	716	658	58
CON	650 (66)	591 (54)	59 (28)

Table 9
Time for J.P. to make a lexical decision (in ms), as a function of prime type and consistency of impairment

	Mean identification time in ms (between-item S.D.)		
	Unrelated word	Related word	Facilitation
Always-impaired	651 (37)	681 (99)	−30 (72)
Usually-impaired	780 (105)	604 (139)	176 (94)

Before accepting this conclusion, however, we wanted to investigate whether J.P.'s priming performance differed for items he could never name as compared to items for which he had been able to accurately name on one or two testing sessions (Table 9). To this end, we conducted an ANOVA with impairment level (always, usually) and prime type (related, unrelated) as within-item factors. This ANOVA indicated an effect of prime type ($F = 17.4$, $P < 0.05$), no effect of impairment type, and a marginal interaction between prime type and impairment type ($F = 7.2$, $P < 0.07$). To rule out the possibility that this was a pattern that CON would show (possibly due to unbalanced factors between the items, because we could not control these for factors, such as word length), we ran an ANOVA as above, but with group (J.P., CON) as a between-items factor. This analysis revealed a significant effect of group ($F = 9.9$, $P < 0.001$), a marginal effect of prime condition ($F = 2.8$, $P < 0.10$), a significant interaction between impairment type and prime condition ($F = 10.1$, $P < 0.01$), and a three-way interaction between group, impairment type, and prime condition ($F = 8.3$, $P < 0.01$). Despite the small sample size, these results suggest that J.P.'s priming was significantly reduced for items that he could never name or access semantic information about, as compared to items that he was sometimes able to name. The magnitude of the priming effects supports this conclusion (Table 9): J.P. showed a priming effect for items on which he was usually-impaired, but not for items on which he was always-impaired.

7. Discussion

The first goal of this study was to examine whether the anterior temporal lobes were required for perceptual repetition priming. To this end, we tested a patient (J.P.), who had bilateral damage to the anterior temporal lobes, on a perceptual repetition priming test using novel verbal stimuli (pseudowords). Consistent with prior patient studies using non-verbal stimuli [62] or proper names [20], J.P. showed normal perceptual repetition priming. This result suggests that the anterior temporal lobes are not required for perceptual repetition priming.

The second goal of this study was to investigate the role of the anterior temporal lobe in conceptual repetition priming. Again, we found that J.P. showed normal performance on category-exemplar priming and masked-form repetition priming, both thought to rely primarily on conceptual as compared to perceptual processes.

It is always difficult to make strong conclusions based on null results, that is, the non-significant interaction term in ANOVAs or non-significant results of *t*-test comparisons. Our ability to detect an impairment for some items on the semantic priming task, however, suggests that the null results on the repetition priming tasks are not likely to have resulted from insufficient power. Further, the fact that J.P. consistently showed priming effects within 1 S.D. of the control participants' mean, and consistently ranked within the middle third of control participants in the magnitude of his priming effects, substantiates the claim that his repetition priming ability was preserved.

Although damage to J.P.'s temporal lobes was bilateral, his lesion was greater in the left-hemisphere than in the right (Fig. 1). This asymmetry leaves open the possibility that the right anterior temporal lobe retained some function that allowed J.P. to perform the priming tasks successfully. It seems unlikely, however, that this asymmetry explains his preserved priming performance because neuroimaging studies have typically found behavioral repetition priming to be associated with decreased activation in left temporal regions [1,7,45,50].

Despite these caveats, the results of this study suggest that although neuroimaging studies indicate that the anterior temporal lobe region is recruited for the performance of repetition priming tasks, it is not required. Although this investigation cannot speak directly to what regions do support repetition priming, the combined evidence from neuroimaging, neuropsychology, and the locus of J.P.'s lesion, suggests that perceptual repetition priming may be supported by more posterior regions, including extrastriate cortex, posterior temporal cortex, and fusiform gyri. Neuroimaging studies have implicated these brain regions in repetition priming [6,7,45,51,75], and patients with damage to occipito-temporal regions are incapable of showing perceptual repetition priming [30]. Although some studies have suggested a right-hemisphere predominance for perceptual repetition priming [17,30], other studies have provided evidence that left-hemisphere processes are sufficient for priming [76].

Conceptual repetition priming likely depends on posterior temporo-parietal regions. These regions have shown priming-related decreases in activation [1,52], and patients with damage to these regions are impaired on conceptual, but not perceptual, priming tasks [28,43]. These posterior regions were spared in J.P., and their preservation likely accounts for his normal repetition priming effects.

This study also examined what effect J.P.'s category-specific semantic deficit would have on his conceptual and semantic priming performance. This analysis allowed us to look more closely at whether J.P. showed abnormal performance based on impaired versus spared categories, or for always-impaired versus usually-impaired items. These breakdowns were important, because a deficit on a small subset of items could have been masked by priming on the remainder of the items. By analyzing J.P.'s performance on spared and impaired items we were able to (a) examine whether his priming was spared, as suggested by his performance when collapsing across all categories of items, (b) investigate whether J.P. appeared to have automatic access to information that he could not retrieve explicitly, and (c) examine whether his pattern of performance differed for tasks of conceptual repetition priming and semantic priming.

On the two repetition priming tasks that are thought to rely primarily on conceptual processes (category-exemplar generation and masked-form priming), J.P. performed normally. The magnitude of his priming was equal to that of control participants, and there was no effect of category type (spared or impaired). In addition, we found no evidence for different priming effects for items on which J.P. was always-impaired as compared to items for which J.P. was usually-impaired. His rankings compared to CON were similar for spared and impaired categories of items. These results support our initial conclusions, namely, that repetition priming was spared in J.P.

This finding suggests that, despite being unable to generate names or semantic information about items explicitly, J.P. retained some representation of those items that could be used in implicit memory paradigms. In particular, we suggest that J.P. may have spared lexical representations, even for items that he cannot explicitly name or provide semantic information about, and that these representations may support his conceptual repetition priming. Our logic for this hypothesis is as follows: category-exemplar generation is thought to rely primarily on conceptual rather than perceptual features [30,63], as is the masked-form repetition task used in this study [14,15]. This conceptual effect does not appear to be reliant on semantic information [15] but rather on lexical representations. Studies with amnesic patients also suggest that intact lexical representations are required for conceptual representation priming: a study with the densely amnesic patient H.M. [46] revealed that he did not show word-stem completion priming if he did not have a premorbid lexical representation of the word. Similarly, normal control participants do not show word-stem completion priming for words that they cannot pronounce correctly (i.e. do not have a lexical representation of [46]).

These results suggest that conceptual repetition priming requires a lexical representation of the word, and does not occur when lexical information is unavailable. If J.P. did not have a lexical representation of the items, we would, therefore, expect him to show impaired priming on the category-exemplar generation or masked-form repetition priming experiments. In contrast, our finding that his conceptual priming effect was normal, even for items on which he was always-impaired on declarative semantic tasks, suggests that he retained a preserved lexical representation of the words.

J.P.'s performance on the semantic priming task showed a different pattern than his performance on the conceptual repetition priming tasks. He showed normal levels of semantic priming overall, for spared and impaired categories. When we compared his priming effect for items on which he was always-impaired versus items on which he was usually-impaired, however, we found that he did not show priming for items he had never been able to name or access semantic information about (always-impaired items) but did show priming for items that he usually was unable to name or access semantic information about (usually-impaired items). This finding differed from the conceptual priming results, where no differences were seen between always-impaired and usually-impaired items in the masked-form priming task.

We suggest two alternatives that could account for this very selective impairment in semantic priming: J.P. may not have had any semantic representations for the always-impaired items, or he may have a severely degraded semantic network for these items. In other words, J.P. may not have shown semantic priming because he no longer had any representation of the always-impaired items. It is also possible, however, that J.P. retained some representation of those items, but that his semantic network was disrupted such that the categorical information was no longer connected to the exemplar, thus preventing semantic priming.

J.P.'s performance on the semantic priming task is not inconsistent with his performance on the repetition priming tasks because the repetition priming tasks do not rely on semantic representations [15], and semantic priming does not appear to be reliant only on lexical representations [10,15,37]; but see [12,57]. Rather, the dissociation between his preserved performance for always-impaired items on the conceptual repetition priming tasks and impaired performance for the always-impaired items on the semantic priming tasks suggests that in J.P., and possibly in other patients with category-specific deficits, the lexical representations of the items may be spared while the semantic representations of the items are degraded or destroyed. This result converges with other evidence indicating that lexical and semantic representations can be stored in different brain regions (for review see [24]).

A caveat must be noted, however: the items used in the conceptual repetition priming tasks were different from those used in the semantic priming task. It cannot be ruled out, therefore, that the dissociation between these tasks arises not because of the reliance on lexical versus semantic representations, but rather because of differences in the particular items. J.P. may have, by chance, retained lexical and semantic representations of items used on the conceptual repetition priming tasks, and neither lexical or semantic representations of items used on the semantic priming task. We do not believe that this explanation fully captures the data, however, because even for items for which J.P. successfully showed priming on the conceptual repetition priming tasks, he still appeared to have a very degraded semantic representation. Even when J.P. showed robust repetition priming for an item, he typically was unable to retrieve any substantial amount of information about that item. For example, although he produced coconut as a fruit on the category-exemplar generation task, he could not correctly determine its color, taste, or how you would eat it. In contrast, for spared items, priming an item would enable him not only to place it in the correct category, but also to be able to explicitly retrieve detailed information about the item, including its color, shape, use, etc.

J.P.'s impairment on the semantic priming task is somewhat consistent with the performance of two patients with semantic dementia [40,69]. These individuals did not show priming for categories, but did for functional properties. It is, therefore, possible that category representations are particularly disrupted, while semantic representations of functional information may be relatively spared [69]. Unlike these patients, however, J.P. did not show overall deficits in semantic priming; his deficits were present only for a small subset of items. His overall semantic priming levels, and his priming for all other item types (spared items, and impaired items which he had been able to name on at least one occasion) was normal.

J.P.'s preserved priming for many items may signify that, for the majority of items, J.P. retains a semantic representation, including categorical information. For these items, his deficit may stem primarily from an access deficit, which was overcome on the implicit, semantic priming, task. In contrast, the items he could never name or generate semantic information about likely no longer have existing semantic representations, or have severely disrupted representations. Thus, for these items, he was unable to show a priming effect on the lexical decision task, on which semantic representations are required.

These analyses must be interpreted with caution because they were conducted on a small subset of items. Nevertheless, they provide putative evidence that patients with category-specific deficits can show access and representation deficits, and that the type of deficit may differ depending on the specific items. Although the dissociation between access and representational deficits appears to be useful in categorizing patients with aphasia, it may be less useful for understanding category-specific semantic deficits. It is possible that the different lesion sites in patients with category-specific semantic deficits versus individuals with aphasia increase the probability of their having a mixed pattern of access and representation deficits.

In summary, this study found that repetition priming was spared in a patient with bilateral lesions that invaded the anterior fusiform gyrus and anterior temporal lobe, even for items about which the patient consistently failed to retrieve information in explicit tests. This result provides evidence that these brain regions are not required for repetition priming based either on perceptual or conceptual information. These regions, however, may be necessary for semantic priming: J.P. showed deficits on this task for at least a small subset of items. J.P.'s preserved performance on the conceptual priming task, together with his impaired performance for always-impaired items (but not other items) on the semantic priming tasks, allowed us to suggest two conclusions. First, we propose that J.P. retains a lexical representation of all items (even items for which he always shows intentional access deficits), but does not retain an intact semantic representation for always-impaired items. Second, we suggest that J.P.'s category-specific deficit does not arise from a pure access deficit or a pure representational deficit; rather, his deficit may result from a combination of these factors, and may depend on the specific item.

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