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Explaining semantic short-term memory deficits: Evidence for the critical role of semantic control

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ABSTRACT

Patients with apparently selective short-term memory (STM) deficits for semantic information have played an important role in developing multi-store theories of STM and challenge the idea that verbal STM is supported by maintaining activation in the language system. We propose that semantic STM deficits are not as selective as previously thought and can occur as a result of mild disruption to semantic control processes, i.e., mechanisms that bias semantic processing towards task-relevant aspects of knowledge and away from irrelevant information. We tested three semantic STM patients with tasks that tapped four aspects of semantic control: (i) resolving ambiguity between word meanings, (ii) sensitivity to cues, (iii) ignoring irrelevant information and (iv) detecting weak semantic associations. All were impaired in conditions requiring more semantic control, irrespective of the STM demands of the task, suggesting a mild, but task-general, deficit in regulating semantic knowledge. This mild deficit has a disproportionate effect on STM tasks because they have high intrinsic control demands: in STM tasks, control is required to keep information active when it is no longer available in the environment and to manage competition between items held in memory simultaneously. By re-interpreting the core deficit in semantic STM patients in this way, we are able to explain their apparently selective impairment without the need for a specialised STM store. Instead, we argue that semantic STM patients occupy the mildest end of spectrum of semantic control disorders.

1. Introduction

The selective disruption of verbal short-term memory (STM) following brain damage has been influential in shaping theories of STM in the healthy brain. In particular, reports of patients showing impaired recall of verbal material in the short-term but essentially normal recall over longer periods (e.g., Warrington & Shallice, 1969) were a major motivation for the multi-component working memory model (Baddeley & Hitch, 1974). These investigations focused on the importance of phonological coding in short-term storage, with a key claim being that "pure" STM patients exhibited impaired phonological storage but no concomitant phonological deficits on other tasks, implying the existence of a phonological store that operates independently of the language production system.

More recently it has become clear that semantic memory deficits are also associated with a marked deterioration in verbal STM (Jefferies, Hoffman, Jones, & Lambon Ralph, 2008; Martin & Saffran, 1997; Patterson, Graham, & Hodges, 1994), in line with evidence for semantic STM coding in healthy individuals (Poirier & Saint-Aubin, 1995; Walker & Hulme, 1999). The involvement of both phonological *and* semantic coding in verbal STM suggests a closer interaction between STM and language processing than has sometimes been assumed, with some researchers proposing that specialised STM stores do not exist and that short-term storage occurs as a result of ongoing activation within the language system (Acheson & MacDonald, 2009; Martin & Saffran, 1997; Ruchkin, Grafman, Cameron, & Berndt, 2003). On this view, deficits in verbal STM arise as a by-product of damage to components of the language system engaged in STM tasks. Therefore, a STM deficit for a particular kind of information (e.g., semantic information) reflects damage to the underlying representations for that kind of information, and this damage should also be detectable on tasks that do not involve STM. In the case of semantic knowledge, this has been demonstrated most clearly in patients with semantic dementia, a neurodegenerative disorder in which knowledge of word meanings gradually deteriorates. Patients with semantic dementia show poorer recall of words that are "unknown" to them as a result of the disease, relative to words they comprehend more fully (Forde & Humphreys, 2002;

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Jefferies, Jones, Bateman, & Lambon Ralph, 2004; Patterson et al., 1994).

Patients with semantic dementia show a STM deficit that is the consequence of a more general degradation of semantic knowledge. In contrast, other studies have revealed patients who have a STM deficit for semantic information but do *not* appear to have semantic deficits on other tasks (Martin & He, 2004; Martin, Shelton, & Yaffee, 1994). The existence of such cases challenges the idea that STM deficits are simply the result of impairments to the language system. Martin et al. (1994) have reported two such patients who presented with normal scores on standard comprehension and picture naming tasks but who were impaired on a number of STM tasks requiring the retention of word meanings. For example, they could accurately sort words into semantic categories when presented with them individually but were profoundly impaired when given a verbally presented list of words and asked whether any belonged in the same category as a subsequent probe. In contrast, their ability to perform an analogous task requiring judgements of phonological similarity was more preserved. Individuals with this pattern of performance have been termed *semantic STM* cases and it has been suggested that their deficits are best explained by a reduction in the capacity of a specialised buffer that holds semantic information in mind over a delay (see also Martin, Lesch, & Bartha, 1999). We refer to this theory as the "semantic buffer" account.

In this paper, we endorse an alternative explanation of the deficit in such patients: that the damage is not to a specialised semantic buffer, but to cognitive control processes that regulate activation in the semantic system (Hoffman, Jefferies, Ehsan, Hopper, & Lambon Ralph, 2009). Our approach is based on the investigations of semantic deficits in certain patients with stroke aphasia, in whom the regulation of semantic memory is disturbed (Jefferies & Lambon Ralph, 2006; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010). We describe these patients more fully later. It is first necessary to say a little about why semantic memory should require cognitive control mechanisms at all. We store a wealth of information about the properties of objects we encounter in the world and typically only a small subset of our knowledge is relevant at any given time. Consider, for example, the two tasks of playing a piano vs. moving a piano across a room (Saffran, 2000). While both involve the same object, a different subset of its properties is germane to each task (functions of the keys and pedals in the former case; its size, weight, value and vulnerability to damage in the latter). Control processes are therefore needed to activate relevant information and inhibit that which is irrelevant for the current context or task. Similar processes are required in lexical–semantic processing. Polysemous words have multiple meanings and to comprehend them the appropriate meaning must be retrieved based on the current context (Rodd, Davis, & Johnsrude, 2005). Even words that are not strictly polysemous can have meanings that vary subtly in different (compare "phases of child development" with "phases of the moon"; Saffran, Bogyo, Schwartz, & Marin, 1980) and in expressive tasks, even highly constrained ones like picture naming, selection between multiple potential responses is required (do I call this image of a four-legged creature "animal", "dog", "Alsatian" or "Fido"?). Appropriate retrieval of semantic knowledge therefore requires a number of regulatory processes, including those that bring task-relevant aspects of knowledge to the fore and those that prevent activation of irrelevant information. This regulation has been termed *semantic control* and neuroimaging studies have associated it with activation in left inferior prefrontal, inferior parietal and posterior temporal cortex (Nagel, Schumacher, Goebel, & D'Esposito, 2008; Rodd et al., 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Patients with lesions to these areas have multimodal semantic deficits arising from poor regulation of semantic knowledge, an impairment we have termed "semantic aphasia" (Corbett, Jefferies, Ehsan, & Lambon Ralph, 2009; Jefferies & Lambon Ralph, 2006; Noonan et al., 2010).

What are the likely consequences of a semantic control deficit for STM tasks that probe semantic knowledge? We propose that there are two functions ascribed to a semantic buffer that are closely linked to semantic control: holding multiple semantic representations in mind simultaneously and maintaining activation of semantic representations internally. Semantic STM tasks, like many comprehension tasks, involve the processing of multiple words in a single trial and require these to be compared with one another on the basis of their semantic properties. Simultaneously maintaining a number of semantic representations is likely to load heavily on the semantic control system. For example, the activation of multiple representations might lead to increased competition between items (Jefferies, Hoffman, et al., 2008). This interpretation has been applied recently to a patient with semantic STM deficit. Hamilton and Martin (2005) found that their patient ML had difficulty inhibiting irrelevant information across a range of verbal tasks and hypothesised that the competition between active representations was the cause of his semantic STM deficit. An additional demand of STM tasks is the need to keep representations of presented stimuli active after those stimuli are no longer present in the environment. Many theories of verbal STM hold that retention occurs by maintaining activation of the units in which long-term linguistic knowledge is coded (MacDonald & Christiansen, 2002; Martin & Saffran, 1997; Ruchkin et al., 2003), perhaps through a process of controlled attention (Cowan, 1995). Successful maintenance depends not only on the relevant linguistic (in this case, semantic) knowledge being intact but also on its activation being appropriately maintained during the delay. Unlike other semantic tasks, where activation could be refreshed by for example re-fixating on the presented picture or word, in a STM paradigm this activation is entirely reliant on internal cognitive control.

These factors predict that, in general, semantic STM tasks should place greater demands on semantic controls than other types of semantic task. For this reason, patients with sufficiently mild semantic control deficits might show impairment on semantic STM tasks while other, less demanding semantic tasks remain relatively unaffected. Though such patients would appear to show a selective deficit for maintaining semantic information, their underlying deficit would be similar to that seen in other patients with impaired semantic control (e.g., semantic aphasia; Jefferies & Lambon Ralph, 2006). If patients with semantic control deficits were arranged on a severity continuum (Martin, 2009), semantic STM patients would occupy the mildest end of the continuum, while patients towards the severe end of the continuum would display deficits on a wider range of semantic tasks.

In line with this theory, in a recent study we found evidence for more general semantic impairments in two patients with semantic STM deficits (Hoffman et al., 2009). The two semantic STM cases, JB and ABU, conformed to the pattern observed in previous patients in that they showed a severe deficit on STM tasks requiring semantic knowledge, but semantic memory more generally was unimpaired on standard tests. However, we also administered some more demanding semantic assessments that did not load on STM, such as generating a verb in response to a noun (Thompson-Schill et al., 1997) and these tasks revealed mild semantic impairments. We directly compared the semantic STM cases with semantic aphasia (SA) patients, who have more severe multimodal semantic deficits arising from impaired semantic control. On the STM tasks they showed a similar, albeit more severely impaired, pattern of performance to the semantic STM cases. On the demanding semantic tasks, the milder cases in this group showed deficits of a similar magnitude as the semantic STM patients. These findings are consistent with the idea that both sets of patients share a common semantic impairment, manifested at different levels of severity.

However, there are two important issues that have yet to be addressed. First, there is no direct evidence that the semantic STM patients' difficulty with demanding semantic tasks is due to their higher control requirements. Second, there is no evidence that the STM deficit has the same root cause as the deficits on other semantic tasks. In the present study, we addressed these two issues in three semantic STM patients with tasks that directly manipulated the level of semantic control required. Two of these tasks were presented in both a visual form and a more demanding STM format, enabling us to test whether similar control deficits were present irrespective of the requirement to use STM. All tasks were previously used by Noonan et al. (2010) to investigate semantic control impairments in a case-series of SA patients. Each task probed a different ability related to semantic control and revealed control impairments in SA patients. The abilities we targeted were:

(1) Resolving ambiguity between potential word meanings (Experiment 1). Processing polysemous words is thought to recruit semantic control processes in order to resolve competition between the possible interpretations of the word and to select the contextually appropriate meaning (Bedny, Hulbert, & Thompson-Schill, 2007; Rodd et al., 2005; Whitney, Grossman, & Kircher, 2009). Noonan et al. (2010) tested SA patients' comprehension of words with multiple meanings and found better comprehension of dominant meanings relative to less commonly used meanings (e.g., they were more accurate when matching *ball* with *bat* than *ball* with *dance*).
(2) Sensitivity to cues that bias semantic processing towards the correct response (Experiment 1). SA patients showed large benefits of external cues that were designed to bias processing towards appropriate semantic representations and away from irrelevant ones. For example, phonological cues substantially improved picture naming performance (Jefferies, Patterson, & Lambon Ralph, 2008), while miscuing with the first phonemes of a semantically related word had a detrimental effect on picture naming, presumably because this increased the activation of competing semantic representations (Noonan et al., 2010). In polysemous word comprehension, sentence cues helped the patients to access the less frequent meanings of homonyms (e.g., when given the sentence "She wore her new dress to the ball", their ability to match *ball* with *dance* improved). This is again indicative of problems regulating access to semantic knowledge. Cues can help in these circumstances because they boost activation of the target representations, enabling them to overcome interference from irrelevant competitors that were activated by the stimulus.
(3) Resisting interference from strong but irrelevant semantic associations (Experiment 2). SA patients are highly susceptible to competition from irrelevant semantic associations. Noonan et al. (2010) demonstrated this using a synonym matching task in which foils shared an irrelevant relationship with the probe (Samson, Connolly, & Humphreys, 2007). Accuracy declined when the foil was strongly related to the target (e.g., matching *piece* with *slice* in the presence of the distractor word *cake*) because the patients selected these strong but task-irrelevant associations. Further evidence for interference from irrelevant but associated information came from an analysis of their picture naming errors (Jefferies & Lambon Ralph, 2006). Patients made a number of associative errors (e.g., squirrel → "nuts"; lorry → "diesel"), suggesting that they successfully activated conceptual information relating to the picture but were unable to select the appropriate response. Finally, the patients showed "refractory access" effects (Warrington & McCarthy, 1983): they were adversely affected when a small set of semantically related items were repeatedly probed (Jefferies, Baker, Doran, & Lambon Ralph, 2007). These presentation conditions encouraged build-up of activation in a set of competing semantic representations, which the patients were unable to resolve.
(4) Detecting associations between distantly related concepts (Experiments 3 and 4). SA patients have difficulty using their semantic knowledge flexibly to determine relationships between items. When matching items on the basis of similarity, they performed well when the items were closely related to each other (e.g., matching *hat* with *cap*) but performed poorly with more distant semantic relationships (Noonan et al., 2010). While closely related items automatically activated highly overlapping semantic representations that were sufficient to detect the match, the distantly related items required more controlled interrogation of semantic knowledge to determine the correct response. In line with this conclusion, on a test of semantic associative knowledge (the Camel and Cactus test; Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000), their performance across trials was influenced by the ease with which the relevant semantic relationship could be determined (Jefferies & Lambon Ralph, 2006).

Our key prediction was that each of these manipulations would influence semantic processing in semantic STM patients, regardless of whether the task had a strong STM component. In the visual versions of the tasks, STM demands were reduced by presenting stimuli as written words, with no time limit on responses and the stimuli present throughout (words were also read aloud by the experimenter). Although these tasks required patients to hold multiple semantic representations in mind on each trial, maintaining this activation was relatively easy because the words were still available in the environment. In Experiments 2, 3 and 4, we contrasted this presentation format with a verbal STM format in which presentation was auditory only. On these tasks, in addition to activating multiple concepts at the same time, activation was entirely reliant on internal cognitive control. Both the semantic buffer and the semantic control hypotheses predicted that the patients would have some difficulty with all of the tasks, because of the requirement to process multiple concepts at once, and that the STM presentation format would be particularly challenging, because of the need to maintain the activation while making a decision. However, the control hypothesis specifically predicted that patients would be more impaired on trials with a high semantic control requirement. These effects would not be expected if the patients' deficits were the result of a reduction in the capacity of a semantic STM store, because the amount of semantic information to be retained (i.e., the number of words presented) was the same in the high and low control conditions of each of our tasks.

2. Case descriptions

JB was a 52 year-old man who left school at the age of 15 and was employed as a factory foreman. He suffered a left-hemisphere haemorrhagic CVA in April 2005. His language profile when assessed four months after the stroke was classified as transcortical sensory aphasia. His speech was fluent and his ability to repeat verbal material was excellent but he displayed marked comprehension and word-finding difficulties. He correctly named seven of the first seventeen items on the Boston Naming Test without cues (BNT; Kaplan, Goodglass, & Weintraub, 1983). We enrolled JB in February 2006, by which time his language skills had improved substantially. There were no obvious abnormalities in his spontaneous speech or comprehension, though he still complained of occasional word-finding difficulties. A structural MRI scan was obtained, which revealed left hemisphere damage in the temporal and parietal cortices. The superior temporal gyrus and sulcus were intact along their lengths and as was the anterior part of

Table 1
Background neuropsychological assessment.

	Max	JB	ABU	JHU	Healthy control mean	Cut-off for normal performance
Visuospatial skills						
VOSP						
Incomplete letters	20	20	19	19	18.8	16
Number location	10	10	10	9	9.4	7
Cube analysis	10	10	9	10	9.2	6
Rey figure copy	36	33	29	NT	34	30
Executive function						
Ravens standard progressive matrices	60	36	34	36	50	27
Brixton test of spatial anticipation	54	42	30	32	37	28
Wisconsin card-sorting test (errors)	128	15	50	57	27	<64

Note: JB's executive function scores are from a more recent testing round than that reported in Hoffman et al. (2009) and suggest some recovery of executive function. NT = not tested.

the temporal lobe. Loss of tissue was primarily along the fusiform and inferior temporal gyri (including the underlying white matter), and to a lesser extent the middle temporal gyrus. There was also a widening of the left sylvian fissure and the posterior horn of the lateral ventricle, which may indicate some additional damage in the surrounding inferior parietal cortex. A more detailed summary of neuropsychological testing for JB and the other patients is given below.

ABU was a 54 year-old man who left school at the age of 15 and was employed as a sheet metal worker for a number of years. He experienced a CVA in June 2003. ABU presented acutely with word-finding difficulty and mild comprehension problems, correctly naming nine of the first 23 items in the BNT (without cues). However, his language abilities recovered after this initial period. When first seen by us in December 2006, his comprehension was good and his speech was fluent though punctuated by occasional hesitations. His phrase length also appeared slightly reduced. He could successfully name 43/60 pictures in the BNT. High-quality structural imaging is not available for this patient. In a CT scan obtained shortly after the CVA, the left lateral ventricle appeared enlarged and the grey-white matter contrast in the basal ganglia was reduced on the left side, which could indicate a diffuse left-hemisphere partial infarction.

JHU was a 74 year-old man who left school aged 15 and spent most of his working life as an estate agent. He suffered a left hemisphere CVA in February 2008 and was referred to us in March 2009. He presented with fluent speech although he had occasional word-finding difficulties. He displayed no comprehension deficits in everyday conversation and he was able to name 45/60 items in the BNT (without cues). Imaging is currently unavailable for this patient.

3. Neuropsychological assessment

3.1. General neuropsychology

Results from background neuropsychological testing are shown in Table 1. Several subtests from the Visual Object and Space Perception battery (VOSP; Warrington & James, 1991) were administered, as was copying of the Rey complex figure (Rey, 1941). These tests revealed good visuospatial function in all patients. Patients also completed three tests of executive function and non-verbal problem-solving, namely Raven's Standard Progressive Matrices (Raven, 1992), the Brixton test of spatial anticipation (Burgess & Shallice, 1996), and the Wisconsin Card-Sorting Test (WCST; Milner, 1964; Stuss et al., 2000). On these tests the patients scored within the normal range for healthy controls, although their scores tended to fall towards the lower end of the range.

3.2. Short-term memory

A detailed assessment of JB and ABU's performance on tests of semantic memory and STM was reported by Hoffman et al. (2009) and is summarised in Table 2. Scores on the same assessments for

Table 2
Semantic and short-term memory assessments.

	Max	JB	ABU	JHU	Controls	
					Mean	Range
Short-term memory						
Digit span						
Forwards	8	7	5	7	6.8	5–8
Backwards	8	4	4	3	4.7	3–7
Letter lists						
Phonologically dissimilar	%	98	74[a]	75[a]	88.3	80–97
Phonologically similar	%	87	41[a]	49[a]	70.7	63–88
Nonword lists	%	57	32	29	28.9	18–46
Word lists	%	80	50[a]	40[a]	69.4	58–87
Size of lexicality effect	%	23[a]	18[a]	11[a]	40.6	34–51
Rhyme judgement span	9	8	6	9	6.98	4.7–9
Category judgement span	7	2.7[a]	2.7[a]	2[a]	6.15	4.7–7
Semantics						
Naming	64	58[a]	63	61	62.3	57–64
Word-picture matching	64	64	61[a]	64	63.8	63–64
Semantic association						
Words	64	62	57	59	60.7	56–63
Pictures	64	59	57	49[a]	59.1	51–62
Category fluency (8 categories)		62[a]	58[a]	56[a]	121.5	75–162

[a] Abnormal scores. Digit, nonword, word and letter lists all involved immediate serial recall with auditory presentation. See Hoffman et al. (2009) for further details of these tests.

JHU are also shown. All patients had forward and backward digit spans in the normal range and could repeat lists of nonwords as accurately as healthy controls (see Hoffman et al., 2009 for further details of these tests). This indicates preserved STM for items maintained using a phonological code. Further evidence for normal phonological coding in STM was seen in the patients' recall of lists of letters. All showed the expected phonological similarity effect of poorer recall of phonologically similar letters. In contrast, phonological similarity effects are reduced in patients with phonological storage deficits (Martin & Breedin, 1992). However, AB and JHU did show an overall impairment in retaining letter lists, indicating the phonological STM is not entirely preserved in these cases.

In contrast, there was clear evidence for impaired STM for semantically mediated information. The “lexicality effect” denoting better recall of real words relative to nonwords is often taken as a marker of lexical/semantic coding in STM (Hulme, Maughan, & Brown, 1991; Jefferies, Hoffman, et al., 2008; Martin et al., 1994). The size of the lexicality effect was reduced in all three patients. AB and JHU had impaired word list recall despite normal memory for nonwords. JB's word list recall fell within the normal range but was lower than expected given his excellent memory for nonwords. Thus, it appears that our patients had difficulty taking advantage of semantic information to aid their recall. Further evidence for this came from semantic category and rhyme probe tasks (Martin et al., 1994). In these, patients were presented with an auditory list of words and decided whether a subsequent probe was related to any of the words in the list. In the phonological condition, judgements were made based on whether the probe rhymed with any of the preceding words, while the semantic condition required patients to decide whether the probe belonged in the same semantic category as any list words. The tasks therefore emphasised memory for either the phonological or semantic characteristics of the words. The results in Table 2 show the maximum list length achieved by the patients in each condition (testing was discontinued when their accuracy fell below 75%). For judgements based on rhyming, patients performed as well as controls, achieving spans of between six and nine words. However, when judgements were made on the semantic criterion of category membership, all patients were severely impaired, failing at lists of between two or three words. This pattern of preserved phonological STM but impaired memory for semantic information has been termed a semantic STM deficit (Martin et al., 1994).

3.3. Semantic processing

Previous studies of semantic STM patients have tested verbal comprehension and single-word production to rule out the possibility that a more general deficit in semantic memory could account for the STM problem. We initially assessed semantic processing using the Cambridge 64-item semantic battery, which probes knowledge of the same 64 living and non-living items across different input and output modalities (Bozeat et al., 2000). The tests included were: (a) Spoken picture naming: the patients were asked to name a black and white line drawing of each item taken from the Snodgrass and Vanderwart (1980) set; (b) spoken word-picture matching: subjects matched spoken names to pictures. On each trial there were nine semantically related foils, all category coordinates of the target. The target and foils were all Snodgrass and Vanderwart (1980) pictures; and (c) semantic association (Camel and Cactus test): a test similar to the Pyramids and Palm Trees Test (Howard & Patterson, 1992) in which subjects decided which of four semantically related items was most associated with a stimulus (e.g., does CAMEL go with CACTUS, TREE, SUNFLOWER or ROSE). There were two versions: in one, the probe and choices were coloured pictures; in the other, they were presented as written words that were also read aloud by the examiner.

These tests suggested that semantic processing was relatively intact in all patients: each patient fell slightly outside the normal range in one test, but otherwise performed well. This apparent preservation of semantic knowledge might give the impression that the patients' deficits were indeed restricted to STM tasks. However, in our previous study we also tested semantic processing in JB and ABU with more demanding speeded comprehension and naming tests in which they were encouraged to respond as quickly as possible (see Hoffman et al., 2009 for details). Both patients showed some evidence of impairment either in accuracy or RT. In addition, a verb generation task provided further evidence of a mild semantic impairment. The full set of tests was not run in patient JHU but Table 2 shows the performance of all three patients on a category fluency test. This task has high cognitive control requirements due to its unconstrained and open-ended nature. In contrast to the other semantic tests, all patients were impaired on this more demanding assessment.

To summarise, all patients showed deficits for semantic information in STM tasks but performed well on standard semantic assessments of the kind typically used to reveal semantic memory impairment. This pattern of spared and impaired function has previously been explained in terms of a specific STM buffer for semantic information (Martin et al., 1994). However, we suggest that the root cause is impairment to cognitive control processes that regulate activation in the semantic system. The present study tested this hypothesis directly by manipulating cognitive control requirements across a range of semantic tasks.

4. Experimental manipulations of semantic control in tasks varying in STM demands

Across four experiments, we explored the prediction that manipulations of semantic control would influence semantic processing in semantic STM patients. These experiments contrasted demanding STM tasks with visually presented versions of the tasks, and compared the size of these effects in the patients to healthy controls.

4.1. Control participants

Seventeen healthy participants were recruited from the Neuroscience and Aphasia Research Unit volunteer panel to take part in this study. They had a mean age of 63.6 years and had completed 13.8 years of education on average. Eight participants took part in Experiment 1 and also completed the tasks in Experiments 2 and 3 under visual presentation. The remaining nine completed the STM tasks in Experiments 2 and 4.

4.2. Statistical analyses

We compared the performance of our patients as a group to that of controls using ANOVA. We also considered the performance of each patient individually. Our key prediction in each experiment was that patients would be particularly impaired in conditions with high semantic control demands. To test this prediction, where possible we used Crawford and Garthwaite's (2005) Unstandardised Test for Differences to determine whether the difference between high and low control conditions in each patient exceeded that observed in the control group. In some cases, however, we were unable to apply this test because all of the controls scored 100% correct in the low control condition. In addition, Crawford and Howell's (1998) modified *t*-test was used to determine whether patients were significantly impaired on each task as a whole.

5. Experiment 1: resolving semantic ambiguity and the influence of cueing

This experiment examined comprehension of the dominant vs. less common meanings of homonyms. When homonyms are encountered, possible meanings are activated simultaneously and compete for selection (Onifer & Swinney, 1981; Rodd, Gaskell, & Marslen-Wilson, 2004; Simpson & Burgess, 1984). Control mechanisms are required to bias processing towards the appropriate interpretation of the word and this control function is particularly important when a more unusual meaning must be selected in the face of strong competition from the dominant interpretation of the word (Bedny et al., 2007; Rodd et al., 2005). Noonan et al. (2010) tested comprehension of homonyms in patients with semantic control deficits. Patients were required to match the target word to a semantically related word, which related to either the dominant or the less common meaning of the word. In some cases the word was presented in a sentence that cued that appropriate meaning and on other trials the sentence cued the alternative meaning (see Fig. 1A). Overall, patients performed better with dominant meanings, as expected if control plays a more important role in accessing less common word meanings. This effect also interacted with cue consistency. When sentence cues were inconsistent with the relevant meaning, performance for the less common meanings was particularly affected, in line with increased competition from the dominant meaning activated by the cue. However, when provided with sentences that cued the appropriate meaning, performance improved and the difference between dominant and less common meanings was virtually eliminated. These sentences boosted activation of the relevant meaning, reducing the competition between meanings and allowing less common interpretations to be retrieved. If our semantic STM patients suffer from a semantic control deficit, we would expect them to show a similar advantage for dominant word meanings in the face of inconsistent sentences. Meaning-consistent sentence cues, on the other hand, should boost comprehension of less frequent interpretations.

5.1. Method

We employed the semantic ambiguity task devised by Noonan et al. (2010). Participants were asked to select which of four words was related in meaning to a probe word. The probe was printed on a page with the four choices beneath; these were also read aloud by the experimenter. In half of the trials, the target referred to the dominant meaning of the probe word (FIRE → HOT). The other trials featured associations based on a less common meaning of the probe (FIRE → RIFLE). There were thirty ambiguous probe words, each presented four times in total. The same distractors were used in both the dominant and less common trials for each probe; none of the distractors were related to either meaning of the probe. Each trial was preceded by a sentence that was either consistent with the meaning of the probe (e.g., for the FIRE → HOT trial: "*I lit a fire*"), or consistent with the alternative meaning ("*Fire at will*"). Sentences were presented in a written format immediately before each trial and were also read aloud. Instructions and practice trials emphasised that the task was to find the word related to the probe, not to the sentence, and that the sentence would sometimes not be helpful. Testing was completed over two sessions, with both meanings of each probe word tested once in each session.

5.2. Results

5.2.1. Group level

Accuracy in each condition is shown in Fig. 2. We compared comprehension in the patients to that of healthy controls using an ANOVA with dominance and cue type included as within-subjects factors and participant group as a between-subjects factor. This revealed main effects of group ($F(1,9) = 65.6$, $p < 0.001$), indicating poorer comprehension in the patients, as well as effects of dominance ($F(1,9) = 21.6$, $p = 0.001$) and cue type ($F(1,9) = 52.3$, $p < 0.001$). Interactions between group and dominance ($F(1,9) = 7.79$, $p < 0.05$)

	Less Semantic Control	More Semantic Control
A Resolving Ambiguity	"I need some more ink for my pen" pen trumpet **pencil** breeze whale	"They herded the sheep into the pen" pen trumpet **enclosure** breeze whale
Effect of Cueing	"She wore her new dress to the ball" ball phone **dance** throat seat	"He tried hard to catch the ball" ball phone **dance** throat seat
B Ignoring Irrelevant Associations	grease hair **oil** basis	dragon fly **monster** melody
C Semantic Distance: visual presentation	leopard **lion** rose coconut	leopard **octopus** rose coconut
D Semantic Distance: STM task	"train, shirt, leopard" Probe: lion? Correct response: **Yes**	"train, shirt, octopus" Probe: lion? Correct response: **Yes**

Fig. 1. Semantic control manipulations. The correct response in each case is shown in bold. (A) More semantic control is needed when an infrequent interpretation of the target word must be accessed. This is particularly the case when the sentence cue primes the alternative word meaning. (B) More semantic control is needed when a distractor word shares a strong association with the probe (e.g., *dragon* and *fly*). (C) More semantic control is needed when the target is only weakly related to the probe. (D) Verifying that the list contains a match for *lion* (i.e., another animal) requires more control when the target and probe are weakly related.

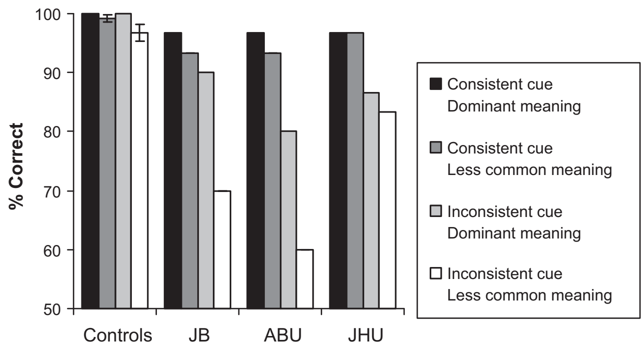

Fig. 2. Semantic ambiguity task (Experiment 1). Bars indicate standard error of control mean.

and group and cue type ($F(1,9) = 39.1$, $p < 0.001$) were also significant, reflecting larger effects of these manipulations in the patients. Finally, there was an interaction between dominance and cue type ($F(1,9) = 17.3$, $p < 0.005$) and a three-way interaction between these factors and group ($F(1,9) = 7.54$, $p < 0.05$), reflecting the fact that meaning dominance had a greater impact for inconsistent cues and that this effect was greater in the patients.

5.2.2. Individual patients

Each patient was impaired on the task as a whole when analysed individually (modified t-test: $t(7) > 7.2$, $p < 0.001$). All three patients showed significantly better comprehension with consistent sentences (McNemar one-tailed $p < 0.05$). Crawford and Garthwaite's (2005) Unstandardised Test for Differences indicated that all three patients showed larger effects of the cue type than controls ($t(7) > 4.8$, $p < 0.003$). In addition, JB and ABU both showed poorer comprehension of less common meanings (McNemar $p < 0.05$ for both patients) while there was no such effect for JHU. We were unable to assess whether these effects were larger than in the control group, as none of the controls made any errors in the comprehension of dominant meanings.

5.3. Discussion

Patients with semantic STM deficits showed effects of cueing in their comprehension of ambiguous words and two of the three patients displayed better comprehension of more dominant meanings. They were almost as accurate as controls when the appropriate meaning was cued by a preceding sentence. However, performance declined when a competing meaning was primed by the sentence cue. In JB and ABU, this effect was more pronounced when the meaning to be retrieved was infrequent and therefore a weak competitor to begin with (though JHU did not show this interaction). These results mirror those seen in semantic aphasic patients with semantic control deficits and suggest that semantic STM patients have difficulty resolving interference between competing semantic representations. These results would not have been expected if the patients' deficits stemmed from damage to a semantic buffer, as the amount of information to be processed was held constant across conditions. It is also important to consider the impact of a semantic buffer deficit on the processing of the sentence cues. If the patients had a reduced capacity for storing semantic information, they would have been unable to process the cues efficiently. The fact that we observed significant differences between the consistent and inconsistently cued trials indicates that this was not the case. The patients were strongly influenced by the semantic information in the sentences, suggesting that they were able to process and retain this information.

6. Experiment 2: resisting interference from strong but irrelevant associates

Experiment 2 investigated the patients' ability to ignore information that was related to the concept being probed but irrelevant to the task. The ability to focus on relevant aspects of knowledge while avoiding interference from irrelevant information is considered to be a key semantic control function (Badre & Wagner, 2002; Thompson-Schill, Bedny, & Goldberg, 2005). Samson et al. (2007) tested this ability in a patient with a semantic control deficit using synonym and antonym judgement tasks in which one of the distractor words shared an irrelevant relationship with the probe (see Fig. 1B). The patient often selected the related distractor rather than the target, particularly when the irrelevant probe–distractor association was stronger than the relationship between target and probe. Noonan et al. (2010) found similar results using the same tasks in a larger group of semantic aphasia cases. These errors can be explained by damage to control mechanisms that bias semantic processing towards task-relevant information. Because of the presence of irrelevant semantic relationships, this task has a strong intrinsic control component, as participants must focus on the appropriate relationship. This is particularly difficult when the probe–distractor relationship is stronger than the probe–target relationship. If semantic STM patients have semantic control deficits that affect their ability to bias semantic processing towards task-relevant information, we would expect them to be impaired on this task generally, even when STM demands are low, and most impaired when the probe–distractor associations were strong. If their STM deficit was due to damage to a semantic buffer, overall impairment on the task would be seen, particularly in the STM condition, but effects of distractor type would not be observed as the number of items to be retained was the same across conditions.

6.1. Method

We used materials from Experiment 2 of Samson et al. (2007). Participants were presented with a probe word and decided which of three words had a similar meaning. In addition to one of the choice words being a synonym of the target, another semantically related but irrelevant word was included as a foil. For example, the probe PIECE was presented with the target SLICE and was accompanied by CAKE (associated foil) and RESIDENT (unrelated foil). Word association norms were used to manipulate the strength of association between the probe and the related distractor (see Samson et al., 2007 for further details). On half of the trials, the probe and target shared a strong relationship and the relationship to the distractor was weak. On the remaining trials this was reversed and the distractor was more strongly related to the probe than the target. There were 84 trials in total.

Two versions of the task were administered, each using the same materials. In the visual version, the probe and three choices were printed on a piece of paper that remained in view until the participant responded (verbally or by pointing). In the STM version, the three choices and probe were read aloud by the experimenter at a rate of one word per second but there was no visual presentation. Participants made a verbal response. Patients completed the two versions of the task in a counterbalanced fashion over two sessions at least a week apart. Each probe was presented once per session. In the control group, a between-subjects design was used such that participants only completed one version of the task.

The task was explained using easy practice examples that emphasised the need to focus on synonyms and not other associations (e.g., FIELD with MEADOW not COW). Patients were also reminded of the instructions midway through each session.

6.2. Results

6.2.1. Group level

Results for the visual and STM versions of the task are shown in Fig. 3. Each version of the task was analysed separately as they were completed by different sets of control participants. A 2 × 2 (distractor type × group) ANOVA conducted on the visual data revealed main effects of distractor type ($F(1,9) = 28.7$, $p < 0.001$) and group ($F(1,9) = 16.4$, $p < 0.005$) as well as an interaction ($F(1,9) = 9.44$,

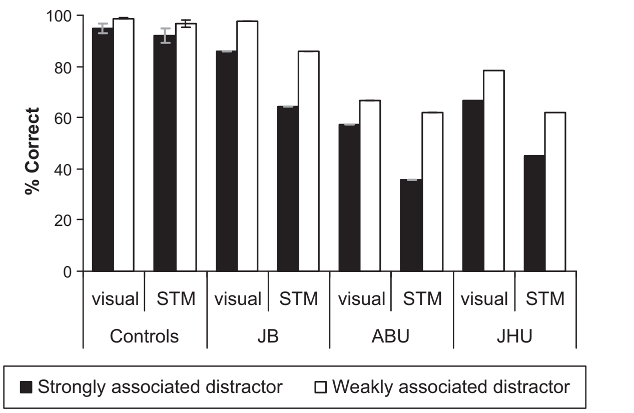

Fig. 3. Ignoring irrelevant associations task (Experiment 2). Bars indicate standard error of control mean.

$p < 0.02$). This reflects the fact that the patients were less accurate than controls and that, while patients and controls were both more likely to make errors when words were accompanied by strongly related distractors, this effect was more pronounced in the patients. Similar results were obtained when the STM data were analysed (distractor type: $F(1,10) = 33.2$, $p < 0.001$; group: $F(1,10) = 35.6$, $p < 0.001$; interaction: $F(1,9) = 11.9$, $p < 0.01$).

6.2.2. Individual patients

When each patient was considered individually, they were all impaired on the STM version of the task ($t(8) > 2.8$, $p < 0.01$) though only ABU and JHU were impaired when the task was presented visually ($t(8) > 7.3$, $p < 0.001$). Overall, all patients were more accurate with visual presentation (McNemar one-tailed $p < 0.05$).

The Unstandardised Test for Differences indicated that, for the STM test, JB and ABU showed larger effects of distractor type than controls ($t(8) > 2.8$, $p < 0.05$), with the effect in JHU falling just short of statistical significance ($t(8) = 2.08$, $p = 0.07$). On the visual task, none of the patients showed a significantly exaggerated control effects when considered individually ($t(7) < 1.7$, $p > 0.14$). However, it is worth noting that the earlier ANOVA indicated that the patients showed a larger effect than controls when considered as a group, so the null results at the individual subject level most likely reflect a lack of power and the fact that the manipulation had a more subtle effect on the visual task.

Finally, we also examined whether the patients selected the related or unrelated distractor when they made an error. JB chose the related distractor on 6/7 errors in the visual test and 17/18 errors on the STM test. ABU chose the related distractor for 29/32 errors under visual presentation and on 34/41 occasions during the STM test. For JHU, the respective figures were 22/23 for the visual test and 33/36 for STM.

6.3. Discussion

All patients showed impaired ability to ignore irrelevant semantic associations, consistent with an underlying semantic control deficit. This effect was present irrespective of whether the stimuli were presented visually or had to be retained in STM, indicating that impaired semantic control affected both STM and non-STM performance.

7. Experiment 3: detecting associations between weakly related concepts

This experiment tested our patients' ability to access semantic knowledge flexibly in order to detect associations between weakly related concepts. Neuroimaging studies have shown that detecting weak semantic associations produces greater activation in inferior frontal and posterior temporal regions involved in semantic control (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Wagner et al., 2001). Noonan et al. (2010) demonstrated that this ability was impaired in patients with semantic control deficits using a similarity matching task in which the semantic "distance" between target and probe was varied. Patients were more likely to detect the relationship when the target and probe were very similar and shared numerous semantic features (e.g., HAT and CAP) than when their association was weaker (e.g., HAT and STOCKING; see also Fig. 1C). Because strongly related items activate very similar semantic representations their relationship was detected with little need for controlled processing. When the association was weaker, greater control was needed to activate the relevant shared attributes to determine the relationship. Here, we tested the ability to detect weak semantic relationships in our semantic STM patients.

7.1. Method

We used the semantic distance task described by Noonan et al. (2010). Participants were presented with the probe word printed on a sheet of paper above three choices: a target and two unrelated distractors. All of the words were also read aloud by the experimenter and the participant was asked to select which item was most similar to the probe. The probes consisted of 64 concrete nouns from eight categories (animals, birds, plants, fruit/vegetables, tools, clothes, vehicles and household objects). Each probe was paired with one target that was very closely related to it and another that shared some similarity but was more distantly related (e.g., GRAPE was paired with CHERRY and CAULIFLOWER). Although these items were drawn from eight categories, subjects were not informed of the categories used in the test and were not instructed to make their judgements on the basis of category membership; they were simply asked to indicate which item was most similar to the probe. Each probe was presented once with the close and once with the distant target and on both occasions with the same two unrelated distractors. Each target appeared as a close match to one probe and as a distant match to another, ensuring that items in close and distant conditions were equal in their familiarity and their category typicality. Testing was completed over two sessions, with each probe presented once per session.

7.2. Results

7.2.1. Group level

Results are shown in Fig. 4. A 2 × 2 (semantic distance × group) ANOVA revealed effects of distance ($F(1,9) = 39.6$, $p < 0.001$) and group ($F(1,9) = 70.3$, $p < 0.001$) and a highly significant interaction ($F(1,9) = 24.0$, $p = 0.001$), indicating that patients had particular difficulty on distantly related trials.

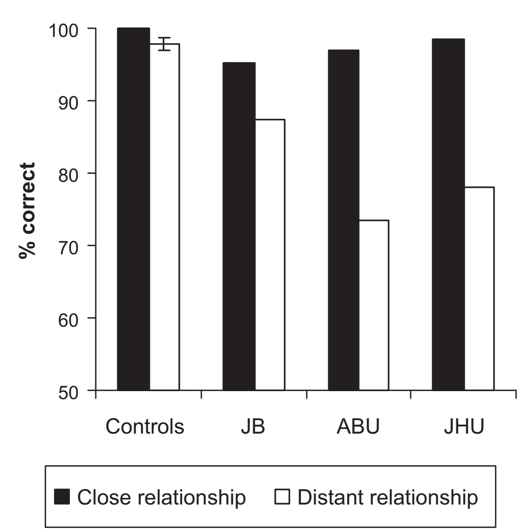

Fig. 4. Semantic distance task with visual presentation (Experiment 3). Bars indicate standard error of control mean.

7.2.2. Individual patients

Overall, each patient was impaired when assessed individually ($t(7) > 5.3$, $p < 0.001$). Two patients were significantly worse at detecting distant relationships (McNemar one-tailed test; ABU: $p = 0.001$; JHU: $p < 0.001$) and a similar trend was observed for JB ($p = 0.09$). We were unable to assess whether the semantic distance effect of each individual patient was larger than that found in the control group, because none of the controls made any errors in the close condition.

7.3. Discussion

Semantic STM patients were able to match semantically related items when they were very similar but had more difficulty when the semantic relationship between the items was weaker. The STM demands were similar in the two conditions of the task, since the same number of items were presented and held in mind in order to make a semantic decision. The patients' deficits on this task most likely reflect impaired semantic control processes, as more control was needed to interrogate semantic information flexibly and detect the more distant semantic relationships (Noonan et al., 2010).

8. Experiment 4: strength of semantic relationship in a STM task

The final experiment investigated the effect of semantic distance in an auditory-verbal STM task. We included the semantic distance manipulation in a standard test format used to identify semantic STM deficits: Martin et al.'s (1994) category probe task. Patients were presented with an auditory list of items followed by a probe and verified whether the probe belonged to the same semantic category as any of the list items. The criterion of category membership is necessary in this paradigm to give subjects a basis on which to decide whether two items match. However, it is easy to find pairs of items that belong to the same superordinate category but are rather distant in semantic space (e.g., *lion* and *octopus*, which are both animals but are different in many ways) as well as those that are very closely related (e.g., *lion* and *leopard*; see Fig. 1D). In addition to varying the semantic distance between the probe and target, we varied the number of items in the list. The semantic buffer hypothesis predicted that list length would be the main determinant of performance, since a reduction in the capacity of the buffer would affect the patients' memory for long lists. In contrast, we predicted that semantic distance have a strong effect on performance. The logic was the same as for Experiment 3: we assumed that the degree of similarity between items would guide subjects' decisions and that patients would have particular difficulty in detecting more distant matches, because these require more controlled, flexible access to semantic knowledge.

8.1. Method

The task featured the same pairings of probes with close and distant targets as in Experiment 3, but in a probe verification task commonly used to detect semantic STM deficits. Participants were presented with an auditory list of words presented at a rate of one per second. This was followed by a pause of 1.5 s and then by a probe word. They were asked to decide whether the probe belonged to the same category as any of the items in the list. On half of the trials the probe shared a category with one list item while on the remaining trials there was no match. For matching trials, each list was presented twice, once with a closely related target (e.g., list: LORRY, CHERRY, SKIRT; probe: GRAPE) and once with a target that was more distantly related but still belonged to the same category (e.g., list: LORRY, CAULIFLOWER, SKIRT; probe: GRAPE; the relevant category in this case being *fruits and vegetables*). Apart from the target, lists were identical in the close and distant conditions so that the information to be remembered was the same in both conditions but in the distant condition participants had to detect a more remote semantic relationship. In addition, to exclude the possibility that targets in one condition were less typical of their category, we obtained typicality ratings from Morrow and Duffy's (2005) norms for 85% of the targets. There was no difference in typicality between close and distant conditions ($t(161) = 0.38$, $p = 0.7$).

To avoid floor and ceiling effects, patients and controls were presented with lists of different lengths. We constructed lists of one, two, three, four, six and seven items, with 64 lists at each length. Patients received all of the lists of lengths one to four and controls completed lengths three to seven. Prior to beginning each testing session, all participants completed a sorting task to ensure that they were familiar with the test items and the categories to which they belonged. For this, the names of the eight categories were printed on cards and placed in front of the participant. They were given a stack of 128 cards, with a word from the test printed on each, and were asked to place each card next to the category it belonged in. All errors were corrected by the experimenter. During the test, the list of categories was also available for patients to consult between trials if they wished. Finally, there were two pairs of categories that were closely related and could have led to confusion (animals vs. birds; plants vs. fruits and vegetables). We avoided using items from these categories together where the outcome could have been ambiguous (e.g., when the probe was an animal, we did not present any birds in the list).

8.2. Results

8.2.1. Group level

In order to compare patients and controls directly, results were divided into three bands: lists of one and two items (completed by patients only), three and four items (by patients and controls) and six and seven items (controls only; see Table 3). We directly compared the performance of patients and controls on the lists of three and four items that all subjects completed. A 2 × 2 (semantic distance × group) ANOVA revealed effects of distance ($F(1,10) = 38.9$, $p < 0.001$) and group ($F(1,10) = 45.2$, $p < 0.001$) as well as an interaction ($F(1,10) = 13.8$, $p < 0.005$), indicating the patients were more strongly affected by the semantic distance manipulation. It is also worth noting that controls showed weak effects of semantic distance on the longest lists. We carried out a 2 × 2 within-subjects ANOVA on the control data, with list length (3 and 4 combined vs. 6 and 7 combined) and semantic distance (close vs. distant) as within-subjects factors. This revealed main effects of length ($F(1,8) = 47.1$, $p < 0.001$) and distance ($F(1,8) = 29.6$, $p = 0.001$) but no interaction ($F < 1$). Therefore, even when overall accuracy in controls was reduced by presenting very long lists the distance manipulation had a relatively small effect.

8.2.2. Individual patients

All patients were largely accurate at rejecting trials in which the probe did not match any of the list items. They were also proficient at detecting a match between a probe and list item when they shared a close semantic relationship but performance declined considerably when the relationship was more distant. McNemar tests indicated that all patients were more likely to detect close semantic matches than distant ones (McNemar one-tailed $p < 0.01$). Modified *t*-tests indicated that all three patients were impaired in their ability to detect matching items ($t(8) > 3.4$, $p < 0.005$). In addition, JB and ABU showed a larger effect of the distance manipulation than did controls when assessed individually ($t(8) > 3.0$, $p < 0.02$). The effect was not larger in JHU. Finally, only one patient (JHU)

Table 3
Semantic distance task in short-term memory (Experiment 4).

List length	Trial type	Control mean (s.d.)	JB	ABU	JHU
1 and 2	No match		97	95	97
	Close match		97	91	97
	Distant match		59	25	75
3 and 4	No match	95 (3.0)	100	84	100
	Close match	94 (4.4)	91	81	72
	Distant match	87 (9.0)	47	50	56
6 and 7	No match	85 (7.2)			
	Close match	73 (13.4)			
	Distant match	63 (15.1)			

showed an effect of list length, performing more poorly on longer lists ($\chi^2 = 4.88$, $p < 0.05$).

8.3. Discussion

Here, we found evidence for impaired semantic control in a standard probe verification task that is commonly used to identify semantic STM impairment. As expected, patients were impaired on this task as a whole. However, this impairment was largely due to an impaired ability to detect weak or distant semantic relationships: patients performed much better when the probe and target was very similar or when there was no relationship present. This indicates that the critical factor influencing the patients' semantic STM deficits was not the amount of semantic information they had to retain but rather the cognitive control demands of performing the necessary semantic judgement.

We have assumed in this explanation that subjects completed this task on the basis of similarity – that they compared the probe to each list item and decided whether any of them were sufficiently similar to warrant a "yes" response. It is worth considering briefly whether an alternative strategy might have been used. Since subjects were told to match items from the same category, it is possible that they might have generated the category label for each item as it was presented and then compared their memory for the categories (rather than the items themselves) to the category label for the probe. However, this possibility provides no explanation for the observed semantic distance effects. The categories were the same in both conditions and the items were matched for typicality, so accessing the category information was equally easy on close and distant conditions. Since patients showed robust effects of semantic distance and controls showed much smaller but similar effects, we can conclude that the similarity of target and probe was an important factor in performing the task and that patients were impaired in dealing with weakly related targets and probes.

9. General discussion

This study investigated semantic control in three patients who showed specific difficulty in maintaining semantic (but not phonological) information in STM. Rather than damage to a dedicated STM buffer for lexical–semantic information, we hypothesised that the root cause of these patients' deficits was a more general impairment in executive control processes that regulate activation in the semantic system (i.e., semantic control). Three key findings emerged across experiments that probed different aspects of semantic control. First, all three patients showed signs of impairment on semantic tasks with minimal STM requirements. Second, the patients were more impaired in conditions that placed greater demands on semantic control. Third, these control effects were present for both STM tasks and visual tasks. These findings are consistent with the view that STM deficits for semantic information arise as a consequence of poor cognitive control over semantic activation. This problem is not specific to STM tasks. However, STM tasks are disproportionately affected as they have high control demands: they require activation of a number of semantic representations to be maintained simultaneously in the absence of the original stimulus.

According to this view, rather than a distinct disorder, semantic STM deficits are seen as occupying the least impaired end of a continuum of semantic control disorders. Other patients who have more pronounced semantic control impairments (referred to here as "semantic aphasics") have the same underlying disorder but appear towards the more severe end of the spectrum. In line with this conclusion, Noonan et al. (2010) showed that SA patients were also sensitive to each of the control manipulations employed in the present study, though their overall levels of performance were lower than those of semantic STM cases. We also found small effects of control manipulations in healthy individuals. This is unsurprising and simply indicates that semantic control plays an important role in processing meaning in the unimpaired system in order to generate time- and task-appropriate behaviour (see Section 1 and also Corbett et al., 2009; Noonan et al., 2010). It should be noted, however, that even on very demanding tasks (e.g., lists of six and seven words in Experiment 4) the sizes of these effects were smaller than those seen in SA and in our semantic STM cases.

Our findings are less consistent with the idea that semantic STM impairments reflect damage to a STM buffer specialised for the temporary retention of semantic information (Martin et al., 1994). The predictions of this theory depend to some extent on the assumed effects of damage to the buffer. If damage principally affected the capacity of the buffer (i.e., the number of semantic representations that can be maintained simultaneously) then no control effects would be expected because this factor was held constant across conditions in all of our tasks. Damage to a buffer might also affect the duration over which semantic information can be held in an active state (i.e., rapid decay of information; see e.g., Martin & Saffran, 1997). The duration of presentation was the same across conditions, so this does not provide a parsimonious explanation of the observed control effects. However, there may have been some subtle differences in the time course of trials: it might take longer to arrive at a correct decision on the high control trials, with the result that patients had difficulty maintaining activation of the relevant semantic information for long enough to perform accurately. This possibility should be investigated in future studies.

We should note that there was some variation in results across patients, with JHU failing to show better comprehension of dominant vs. less common meanings and failing to show a significantly larger semantic distance effect than controls in Experiment 4. We interpret this as reflecting individual differences in the susceptibility to particular control manipulations. Noonan et al. (2010) observed some inter-subject variability amongst SA patients in the size of effects on individual tasks, despite a clear pattern of impaired semantic control emerging in the study as a whole. One way to combat this individual variability is to compute group-level statistics as well as evaluating each subject individually. In each experiment, ANOVA revealed that, when considered as a group, the patients showed larger effects of semantic control than healthy individuals. Another approach is to search for a common pattern across multiple tasks that tap different aspects of the cognitive function in question. In this study, we probed four different aspects of semantic control and JHU did show the expected semantic control effects in cueing (Experiment 1), strength of distractors (Experiment 2) and semantic distance (Experiment 3).

Our proposal that semantic STM deficits reflect impaired control of semantic activation is in line with recent investigations of another semantic STM patient (ML) by Hamilton and Martin (2005). Rather than rapid decay of semantic activation, they proposed that the STM deficit in this patient was the result of an underlying failure to inhibit verbal information. ML showed large interference effects in the Stroop task and also in a probe recognition task known as the recent negative task. Here, ML had to decide whether a probe was contained in a list of items presented immediately before. On critical "recent negative" trials, the probe did not appear in the current list but had been presented on the previous trial. ML often incorrectly accepted these probes as being part of the current list, suggesting that activation from the previous trial interfered with memory for the current set. This behaviour is consistent with a cognitive control explanation of this patient's deficit, as inhibition of irrelevant information is a key requirement in regulating semantic knowledge. However, there are a number of reasons why a specific inhibition deficit is unlikely to be a complete explanation of our patients' impairments. We manipulated semantic control demands in a variety of different ways across three experiments, yet the patients showed deficits on high control conditions on all tasks. While Experiments 1 and 2 clearly required inhibition of irrelevant semantic information, the role of inhibition was less clear in Experiments 3 and 4, as here the high control condition featured weak semantic associations but no distracting information. One way in which inhibition may have been important in the Experiment 4 is in ensuring words presented in previous trials did not interfere with the current trial. If the patients' errors resulted from an inhibitory failure, we might expect persisting activation of items from previous trials to generate false positives when there was no matching item in the current list. In fact, the patients' ability to correctly reject trials with no match was very good. One final piece of evidence against inhibition deficits was observed in Experiment 2, which required recall of one of three choice words. Here, our patients never recalled words from previous trials, as would be expected if activation was not inhibited properly (even though other patients with semantic STM deficits have shown this pattern in recall tasks (Martin & Lesch, 1996). On the basis of this evidence, it seems that our patients had a more general problem in regulating semantic information, rather than a specific inhibition deficit.

These divergent findings may point to subtle underlying differences in the nature of the deficit in different semantic STM cases. In fact, while our patients all show the core features of a semantic STM deficit (i.e., poor STM for semantic information with intact phonological STM and no marked comprehension deficit) there are some differences between them and other cases in the literature, most notably with respect to lesion site. Previous semantic STM patients have had damage to the left inferior frontal gyrus (Hamilton & Martin, 2005; Martin et al., 1994), a region frequently associated with semantic selection and inhibition functions (Badre & Wagner, 2005; Nagel et al., 2008; Robinson, Blair, & Cipolotti, 1998; Thompson-Schill et al., 1997, 1998, 2002). In contrast, scanning in our semantic STM cases JB and ABU points to damage centred on posterior temporal and inferior parietal cortex. Although these regions are often overlooked in discussions of semantic control, they are frequently also activated in neuroimaging studies that manipulate semantic control (Badre et al., 2005; Hirshorn & Thompson-Schill, 2006; Rodd et al., 2005; Thompson-Schill et al., 1997; Wagner et al., 2001). In addition, SA patients can present with damage to either inferior frontal or temporoparietal cortex yet show similar patterns of performance on semantic tasks (Berthier, 2001; Noonan et al., 2010). So both neuroimaging and neuropsychological data point to a network of brain regions involved in semantic control, including inferior prefrontal cortex as well as temporal and parietal regions. Our hypothesis, then, is that semantic control deficits can explain semantic STM deficits in patients with prefrontal as well as posterior lesions. However, the differences between our patients and patient ML may indicate a degree of specialisation within the control network, with prefrontal cortex particularly important for resolving interference between competing representations (explaining inhibition deficits in ML) while temporoparietal regions perform a more general control function (explaining control deficits without specific inhibitory problems in JB and ABU). A similar suggestion has been made by Badre et al. (2005) on the basis of neuroimaging data.

Direct comparison of semantic STM patients with different lesions is needed to determine the extent to which all such patients can be said to share a common underlying control deficit. Another important target for future work is to investigate semantically impaired patients who do *not* show a disproportionate deficit on semantic STM tasks. We predict that semantic control would be relatively spared in such cases. The major contribution of this study is to demonstrate that semantic STM deficits can arise as a consequence of a more general cognitive control impairment for semantic information, of the kind seen in a variety of aphasic patients. The existence of semantic STM patients has previously motivated a highly specialised view of STM capacity with multiple dedicated stores (Martin et al., 1994). By linking semantic STM deficits to more basic semantic control processes required across a broad range of tasks, we have shown that these patients are consistent with approaches in which STM capacity is dependent on the architecture of the language system (Acheson & MacDonald, 2009; Martin & Saffran, 1997).

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Appendix A.

Stimuli for Experiment 1.

Probe	Target in dominant meaning condition	Target in less common meaning condition	Distractor 1	Distractor 2	Distractor 3
Scoop	Spoon	Newspaper	Chicken	Sister	Navy
Ball	Goal	Dance	Phone	Throat	Seat
Sock	Stocking	Punch	Bark	Cliff	Stew
Game	Toy	Hunt	Ramp	Sponge	Isle
Arm	Leg	Gun	Glass	Train	Key
Film	Movie	Skin	Coal	Prince	Golf
Leaf	Tree	Page	Sleep	Hat	Dust
Prune	Plum	Shrub	Cube	Mug	Soot
Foot	Base	Measure	Jack	Produce	Style
Pile	Heap	Carpet	Assault	Nerve	Troop
Throw	Pass	Blanket	Weather	Village	Chair
Grade	Mark	Slope	Contact	Kill	Dream
Toll	Bridge	Bell	Snow	Stone	Milk
Pump	Petrol	Shoe	Band	Soil	Kid
Head	Skull	Boss	Fur	Boot	Tar
Lip	Kiss	Edge	Sheet	Joy	Bomb
Plant	Vegetable	Factory	Cellar	Penny	Cream
Deposit	Cash	Dirt	Seed	Yard	Brain
Ear	Sound	Wheat	Flock	Paste	Pork
Blue	Yellow	Sad	Blind	Curve	Shear
Bank	Money	River	Morning	Heart	Child
Juice	Fruit	Fuel	Sheep	Aunt	Laugh
Fire	Hot	Rifle	Dinner	Weight	Poet
Spray	Liquid	Flowers	Slave	Snake	Palace
Scrub	Wash	Bush	Chart	Coach	Gin
Pen	Pencil	Pig	Star	Meadow	Lemon
Yarn	Wool	Fable	Axle	Junction	Ulcer
Beam	Ray	Wood	Pope	Male	Lunch
Bar	Wine	Block	Song	Birth	Dress
Boil	Pan	Sore	Fleet	Ranch	Graph

Stimuli for Experiments 3 and 4.

Probe	Close target	Distant target	Distractor 1 (Expt 3)	Distractor 2 (Expt 3)	Category (Expt 4)
Leopard	Lion	Octopus	Rose	Coconut	Animals
Whale	Seal	Mouse	Mushroom	Apple	Animals
Wasp	Bee	Lion	Daffodil	Bean	Animals
Shrimp	Lobster	Squirrel	Oak	Lemon	Animals
Mole	Mouse	Seal	Ivy	Potato	Animals
Donkey	Horse	Lobster	Fern	Cauliflower	Animals
Chipmunk	Squirrel	Bee	Wheat	Cherry	Animals
Squid	Octopus	Horse	Pine	Beetroot	Animals
Finch	Sparrow	Ostrich	Pine	Coconut	Birds
Magpie	Crow	Eagle	Mushroom	Cherry	Birds
Cockatoo	Parrot	Swan	Wheat	Cauliflower	Birds
Buzzard	Eagle	Gull	Ivy	Bean	Birds
Emu	Ostrich	Crow	Daffodil	Lemon	Birds
Cormorant	Gull	Chicken	Rose	Beetroot	Birds
Goose	Chicken	Parrot	Oak	Potato	Birds
Duck	Swan	Sparrow	Fern	Apple	Birds
Elm	Oak	Wheat	Lion	Swan	Plants
Toadstool	Mushroom	Fern	Horse	Ostrich	Plants
Holly	Ivy	Daffodil	Mouse	Crow	Plants
Daisy	Rose	Oak	Seal	Gull	Plants
Bracken	Fern	Rose	Octopus	Parrot	Plants
Fir	Pine	Ivy	Lobster	Chicken	Plants
Barley	Wheat	Pine	Squirrel	Sparrow	Plants
Bluebell	Daffodil	Mushroom	Bee	Eagle	Plants
Broccoli	Cauliflower	Apple	Lobster	Ostrich	Fruit + veg
Pear	Apple	Potato	Bee	Sparrow	Fruit + veg
Turnip	Beetroot	Cherry	Seal	Parrot	Fruit + veg
Pea	Bean	Lemon	Octopus	Chicken	Fruit + veg
Carrot	Potato	Coconut	Mouse	Eagle	Fruit + veg
Orange	Lemon	Beetroot	Horse	Gull	Fruit + veg
Pineapple	Coconut	Bean	Lion	Crow	Fruit + veg
Grape	Cherry	Cauliflower	Squirrel	Swan	Fruit + veg
Bed	Futon	Table	Sledge	Stocking	Household
Freezer	Fridge	Radio	Aeroplane	Shirt	Household
Shower	Bath	Oven	Canoe	Shoe	Household
Stereo	Radio	Fridge	Pram	Jumper	Household
Chair	Sofa	Rug	Coach	Knickers	Household
Carpet	Rug	Sofa	Motorbike	Cap	Household

Probe	Close target	Distant target	Distractor 1 (Expt 3)	Distractor 2 (Expt 3)	Category (Expt 4)
Cooker	Oven	Futon	Van	Belt	Household
Desk	Table	Bath	Yacht	Mitten	Household
Mallet	Hammer	Strimmer	Coach	Stocking	Tools
Watering can	Hosepipe	Spanner	Yacht	Belt	Tools
Paintbrush	Sandpaper	Rake	Motorbike	Mitten	Tools
Drill	Screwdriver	Spade	Van	Cap	Tools
Wrench	Spanner	Hosepipe	Pram	Jumper	Tools
Lawnmower	Strimmer	Sandpaper	Sledge	Shirt	Tools
Shovel	Spade	Screwdriver	Aeroplane	Shoe	Tools
Hoe	Rake	Hammer	Canoe	Knickers	Tools
Hat	Cap	Stocking	Futon	Spade	Clothes
Pants	Knickers	Jumper	Bath	Screwdriver	Clothes
Glove	Mitten	Shirt	Rug	Strimmer	Clothes
Blouse	Shirt	Cap	Oven	Hammer	Clothes
Cardigan	Jumper	Belt	Radio	Spanner	Clothes
Braces	Belt	Shoe	Sofa	Rake	Clothes
Boot	Shoe	Knickers	Table	Hosepipe	Clothes
Tights	Stocking	Mitten	Fridge	Sandpaper	Clothes
Ship	Yacht	Van	Radio	Hammer	Vehicles
Bus	Coach	Sledge	Table	Sandpaper	Vehicles
Pushchair	Pram	Coach	Sofa	Screwdriver	Vehicles
Helicopter	Aeroplane	Pram	Futon	Spanner	Vehicles
Scooter	Motorbike	Yacht	Rug	Spade	Vehicles
Lorry	Van	Canoe	Oven	Rake	Vehicles
Dingy	Canoe	Motorbike	Bath	Strimmer	Vehicles
Ski	Sledge	Aeroplane	Fridge	Hosepipe	Vehicles

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