

**What Influences The Accessibility Of Conceptual
Knowledge? Evidence from Experimental
Psychology, Neuropsychology and Brain Stimulation**

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Abstract

Previous studies have shown that accessibility of conceptual information declines when sets of semantically-related items are presented repeatedly, although the underlying basis of this effect is debated – it is unclear if comprehension can decline without massed repetition of individual items, or if this effect is restricted to lexical retrieval in picture naming. Furthermore, declining comprehension has been characterised as arising from both ‘too much activation’ (i.e., on-going strong activation of competitors) and ‘too much inhibition’ (i.e., a failure to overcome inhibition which may facilitate the earlier retrieval of semantically-related targets). The thesis explored the impact of experimental manipulations (speed of presentation; strength of association between category and target item; modality of presentation; type of semantic decision required), on the magnitude of declining comprehension in healthy young adults. Comprehension declined even without individual item repetition, especially for strongly-associated targets (which may have accrued more competition or inhibition). The effect was found irrespective of presentation modality and more strongly at fast presentation speeds (when there was less time to overcome competition/inhibition). Next, the thesis examined the impact of ageing and semantic aphasia on changes in comprehension within the continuous categorisation paradigm. In these populations, controlled retrieval of conceptual information is thought to be weakened (relative to younger adults and healthy controls without aphasia). This should exaggerate declines in comprehension that reflect difficulty overcoming competition, but reduce the effect if it arises from the inhibition of competitors on earlier trials. The results were in line with the second hypothesis, since older adults and patients with semantic aphasia maintained their performance throughout the categories, unlike younger adults. Lastly, the thesis examined how this effect is modulated by transcranial electrical stimulation delivered to a key brain region implicated in semantic control – left inferior frontal gyrus (LIFG). Stimulation of LIFG attenuated the effect of declining comprehension, perhaps because initial retrieval was facilitated (potentially reducing the inhibition of related information), and/or because subsequent target selection was strengthened. Together, these results provide a more comprehensive account of what drives declining performance in continuous categorisation in healthy young adults who have the capacity to strongly engage semantic control.

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Declaration

I declare that this thesis is a presentation of original work and has been completed by the candidate under the supervision of Prof. Beth Jefferies and Dr. Hannah Thompson. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Chapter 2 is a revision for a paper submitted to the Quarterly Journal of Experimental Psychology: *'When comprehension elicits incomprehension: Deterioration of semantic categorisation in the absence of stimulus habituation'*. Upasana Nathaniel, Hannah Thompson, Emma Davies, Dominic Arnold, Glyn Hallam, Sara Stampacchia, Jonathan Smallwood and Beth Jefferies.

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Chapter 1

Introduction

Thesis aims and key research questions

The ease with which we can understand or remember a word or a picture depends on our ability to successfully retrieve relevant information from memory. Accounts of both episodic and semantic memory distinguish between accessibility and availability (Johnson & Anderson, 2004; Tulving, 1972); i.e., the difference between a representation being temporarily inaccessible and being permanently forgotten. Within episodic memory, items that are *inaccessible* in standard recall are frequently retrieved successfully in cued recall, showing that these items are still represented (Tulving & Pearlstone, 1966). A parallel view within semantic cognition proposes two interacting core components: (i) semantic *representations* – i.e., the database of stored concepts and their relationships with each other, and (ii) semantic *control* processes – which allow these representations to be directed based on the context or task demands (Jefferies & Lambon Ralph, 2006). Nevertheless, the relationship between these components is poorly understood.

Additionally, our ability to name or remember a word or a concept depends on its connections to other items that are concurrently or recently processed. For instance, retrieval from episodic memory can be impaired following retrieval of a related memory (i.e., retrieval induced forgetting; Anderson, Bjork, & Bjork, 1994); likewise, naming a picture, such as DOG, can either successfully prime a related picture (i.e., repetition priming; Mitchell & Brown, 1988), or naming can be slowed following a semantically related word, such as CAT (i.e., semantic interference; Wheeldon & Monsell, 1994). This effect speaks to the effect of retrieval on the subsequent accessibility of related memories and concepts, and thus potentially the interplay between representations and controlled retrieval processes.

This thesis examines whether the accessibility of conceptual knowledge changes during continuous retrieval, investigates the factors that influence this effect and explores its neural basis. Firstly, continuous semantic categorisation is explored in healthy young adults, using a paced auditory comprehension task. Previous studies have shown that comprehension can decline when sets of semantically-related items are repeated (Wei & Schnur, 2015), and these effects have often been explained in terms of a build-up of competition between the items as they become highly active (Belke, Meyer, & Damian, 2005; Oppenheim, Dell, & Schwartz, 2010; Schnur, Schwartz, Brecher, & Hodgson, 2006). At the same time, lexical retrieval in picture naming has been shown to decline even in the absence of item repetition, and at relatively long intervals between semantically-related trials, in a continuous naming paradigm – this effect has been explained in terms of weight changes between lexical and semantic representations (Howard, Nickels, Coltheart, & Cole-Virtue, 2006; Oppenheim et al., 2010). This interpretation resembles

retrieval-induced forgetting in the domain of language, since in both accounts there is temporary suppression of knowledge as a direct consequence of the retrieval of related information. It is not yet clear if comprehension declines in a similar way, in the absence of item repetition: the research presented here therefore examined a continuous categorisation paradigm, in which factors thought to moderate the effect of prior retrieval on the accessibility of semantic information were manipulated. In particular, the thesis work examines the effect of the strength of association between the target and the category that defined the goal for retrieval. Continuous categorisation might have a particularly detrimental effect on the accessibility of highly-associated conceptual information, and this might be because this information is more strongly suppressed during the retrieval of other relationships to promote flexibility (Oppenheim et al., 2010). The research also examines whether the words for successive categorisation have to be closely semantically-related to each other, or whether it is sufficient that the items share goal-relevant features: this helps to establish whether changes in accessibility are driven by global changes within conceptual representations, or whether these effects reflect the strength of specific links between goal-relevant features and concepts. As well as factors that relate to the structure of knowledge itself, the thesis examines the impact of divided attention, ageing and semantic aphasia on changes in comprehension within the continuous categorisation paradigm. A further study characterises how this effect is modulated by electrical stimulation delivered to a key brain region implicated in semantic control – left inferior frontal gyrus. These investigations explore the impact of variation in the capacity to shape semantic retrieval through the application of control (enhanced by anodal tDCS and reduced by divided attention), plus more complex changes in retrieval that might occur as a consequence of stroke and ageing. In these populations, the retrieval of initial targets is expected to be reduced, as well as in the application of semantic control to maintain appropriate retrieval in the face of building interference.

To put these research aims into context, this chapter will discuss the current literature on semantic retrieval and, in particular, what is known about factors that influence the accessibility of conceptual knowledge. First, the chapter reviews the evidence that semantic representations have a distinct neural basis from processes supporting controlled retrieval. The chapter describes neuropsychological evidence for a dissociation between ‘storage impairments’ (in semantic dementia) and ‘control/access deficits’ (in stroke aphasia). Since patients with semantic control deficits in the context of aphasia have damage to left inferior frontal cortex, the next section discusses converging evidence for the role of this brain region in various aspects of the control of semantic retrieval – including the selection of relevant representations in the face of strong competition, and the ‘controlled retrieval’ of difficult to recover, weakly represented knowledge.

The next section of the current chapter discusses several literatures that have reported retrieval-induced changes in the accessibility of semantic information. The literature on ‘refractory’ effects in patients with aphasia and control/access semantic deficits is reviewed (i.e., temporary reductions in accessibility immediately following semantic retrieval), and the potential connection with fatigue (a common post-stroke sequelae) is discussed. The next section discusses factors influencing the accessibility of knowledge in healthy adults, drawing on multiple disparate literatures: psycholinguistic investigations showing that performance, particularly in picture naming, declines when semantically-related items are repeated; reports of “semantic satiation” following massed repetition and accounts of retrieval-induced changes in memory more widely. While there are some similarities with refractory effects in patients with semantic control deficits, there are also some important differences that are highlighted. The next section considers the possible effects of ageing on the accessibility of conceptual information over time, and considers the possibility that electrical stimulation (anodal tDCS) may be able to boost controlled semantic retrieval and overcome the deleterious effects of continuous categorisation more specifically. Finally, this chapter will outline the key research themes and structure of the thesis.

Neural mechanisms underpinning semantic access

Semantic aphasia vs. semantic dementia: their symptoms and brain basis

One of the core functions of semantic memory is to extract meaning from diverse experiences with items or objects; these range across various modalities, such as written or spoken words, pictures and sounds (Lambon Ralph & Patterson, 2008; Rogers & McClelland, 2004). Semantic memory is thus supported by a heteromodal conceptual system that represents features of the semantic structure, irrespective of modality (Caramazza, Hillis, Rapp, & Romani, 1990; Rogers et al., 2004); semantically similar items are characterised as being closer together within multidimensional semantic space (McClelland & Rogers, 2003). Emerging evidence suggests that a key region for the representation of heteromodal semantic knowledge is in the ventral anterior regions of the temporal lobes (ATL; Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Visser, Jefferies, Embleton, & Lambon Ralph, 2012). This multimodal semantic ‘hub’ is considered to be crucial to understand the deeper semantic relationships between items that may share very few sensory properties, and to connect the multimodal characteristics of each item to allow matching between visual features, sounds, words, smells, etc. (Nestor, Fryer, & Hodges, 2006; Patterson, Nestor, & Rogers, 2007; Williams, Nestor, & Hodges, 2005). The concepts stored within the semantic system (in ATL) can be represented as activated patterns that are distributed over multiple units, which correspond to various features (Tyler, Moss, Durrant-

Peatfield, & Levy, 2000). Thus, similar concepts are represented by similar activation patterns, which enable generalisations to be made about new items (cf. Garrard, Ralph, Hodges, & Patterson, 2001). Evidence that ATL is core to these semantic representations comes not only through semantic dementia patients (discussed below), but also PET studies (e.g., Price, Devlin, Moore, Morton, & Laird, 2005; Rogers et al., 2006), MEG and EEG studies (e.g., Halgren et al., 2006; Marinkovic et al., 2003), and distortion corrected fMRI (e.g., Visser et al., 2012). These heteromodal conceptual representations cannot work without inputs from modality-specific regions, however: category-specific semantic impairments follow from damage to modality-specific regions which are important for distinguishing between concepts within particular categories – for example, motor, praxis and visual motion features may contribute to the representation of tools, while visual features may make a greater contribution to the differentiation of animal concepts (Martin & Chao, 2001; Mollo et al., 2016; Tyler et al., 2000).

From this store of knowledge, semantic control exerts its influence so that only the most appropriate aspects of knowledge are brought to the fore. There are at least two distinct forms of semantic impairments: (i) One results from damage to semantic representations (degraded store impairment) as seen in patients with semantic dementia (SD; Hodges, Patterson, Oxbury, & Funnell, 1992; Jefferies & Lambon Ralph, 2006; Warrington, 1975). (ii) The other results from damage to modality-specific access processes and pathways that spare semantic representations (semantic ‘access’ impairment) as seen in semantic aphasia (SA; Jefferies & Lambon Ralph, 2006; Warrington & McCarthy, 1983; Warrington & Shallice, 1979). Qualitative differences between ‘storage’ and ‘access’ patients, who show deficits of semantic representation and control respectively (with differing sites of brain damage), have been influential in developing theories of semantic processing and representation (Cipolotti & Warrington, 1996; Jefferies & Lambon Ralph, 2006; Jefferies, Patterson, & Ralph, 2008; Lambon Ralph & Patterson, 2008; Warrington & McCarthy, 1983; Warrington & Crutch, 2004).

Atrophy in semantic dementia (SD) is largely restricted to the bilateral anterior temporal lobes (ATL), suggesting that the cognitive disorder in these patients is related to damage in this region rather than a widespread functional abnormality (Diehl et al., 2004; Mummery et al., 2000; Nestor, Fryer, & Hodges, 2006). This focal atrophy, centred on the ventral portion of the ATL, is associated with the degradation of semantic knowledge across modalities (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Coccia, Bartolini, Luzzi, Provinciali, & Ralph, 2004; Garrard & Carroll, 2006; Rogers et al., 2004). On the other hand, deficits that are seen in aphasia include loss or impairment of the ability to produce and/or comprehend language. About 40% of stroke

patients exhibit some degree of aphasia, such as phonological paraphasias (i.e., errors in word form), or semantic paraphasias (errors in word-meaning), and about half of these individuals sustain permanent language disability (Cao, George, Ewing, Vikingstad, & Johnson, 1998). Patients with stroke aphasia can also have comprehension deficits on the same range of verbal and non-verbal tasks as SD patients, but they show a very different pattern of brain damage, centred on left inferior frontal cortex and/or left temporoparietal areas. These patients rarely have damage to the ventral ATL (Jefferies, Baker, Doran, & Ralph, 2007; Thompson, Henshall, & Jefferies, 2016), presumably because this region is watershed territory, supplied with blood by branches of both the middle and posterior cerebral arteries (Phan, Donnan, Wright, & Reutens, 2005; Phan, Fong, Donnan, & Reutens, 2007). The nature of the semantic deficit in stroke aphasia would therefore be expected to be qualitatively different from that in SD, since the central store of amodal conceptual knowledge in ATL should be preserved. In line with this view, patients with poor comprehension in the context of stroke aphasia have been reported to have semantic ‘access’ impairments: i.e., impairment of ‘access’ or retrieval mechanisms; particularly deficits of controlled retrieval in semantic aphasia (SA) that allow non-dominant aspects of knowledge to be the focus of ongoing cognition (Jefferies & Lambon Ralph, 2006).

Evidence for this view was provided by a case-series comparison of SD and SA patients on a range of semantic tests (Jefferies & Lambon Ralph, 2006). It was found that despite their very different areas of brain damage, SD and SA patients displayed similar degrees of impairments on verbal and nonverbal semantic tasks. Nevertheless, there were qualitative differences in the nature of their semantic impairments, reflecting a deterioration of knowledge in SD, and deregulated semantic control in SA. The SD patients exhibited performance that was consistent across the different semantic tasks; they were able to retain knowledge of an item and demonstrate this from one task to another. However, SA patients were often unable to retrieve information about items they had understood in other tasks with different control demands, such as word-picture matching vs. judgements of semantic associations, and showed consistency or significant correlations only between different versions of the same semantic task, such as judgements of semantic association for pictures and words. In addition, patients with SD showed bigger effects of item familiarity or frequency, in contrast, SA patients were not as affected by this factor, instead their ability in making judgements based on semantic associations was affected by how easily the required association could be discerned and how readily they could reject competitors. Further insight into the underlying disorder in SD and SA patients comes from the errors they produce on a picture-naming task. Frequent super-ordinate or coordinate semantic errors were made by the SD group, for example, producing “animal” or “dog” for SQUIRREL, while

the SA patients made associative errors, such as producing “nuts” for SQUIRREL, which were almost never seen with the SD patients. The ability to generate such errors revealed that a surprising amount of knowledge was still retained in patients with semantic aphasia; however, their difficulties lie in directing activation toward the correct response and away from the task irrelevant associations. Moreover, the SA group benefitted from phonemic cues in naming pictures, more than the SD patients. The use of cues provided the additional external constraint needed on semantic activation, and reduced the internally generated control (Jefferies et al., 2008).

Other research has supported the view that patients with aphasia following left frontal lesions have deficits of controlled semantic retrieval. In one study, when the strength of association between the cue and target was strong, SA patients with damage to LIFG indicated typical priming effects (Blumstein, Milberg, & Shrier, 1982), but they failed to exhibit normal priming when the strength of association between pairs was decreased (Milberg, Blumstein, & Dworetzky, 1987). In a single patient study following resection of a left frontal glioma, more errors for weakly related items in comparison to strong associations were found, in addition, the patient also presented with inconsistency in retrieving relevant concepts (Campanella, Crescentini, Mussoni, & Skrap, 2012). Similar difficulties were also found using homonyms (i.e., words with several meaning depending on the context; Bedny, Hulbert, & Thompson-Schill, 2007). Furthermore, patients with a focal damage to the inferior prefrontal regions were affected in their capacity to generate verbs from nouns, but only in condition with high selection demands (Thompson-Schill et al., 1998). For example, LIFG damage was associated with deficits in generating words in control-demanding situations, such as producing a verb for the noun DOG (i.e., high demand as there is no strongly-associated action) in contrast to a noun with lower demands (e.g., SCISSORS, one with strongly associated action “cut”). Also, the ability to produce sentences for stimuli that have several conceptual propositions and thus need to compete for selection was also found to be impaired in patients with frontal damage (Robinson, Shallice, & Cipolotti, 2005). This impairment of tasks with high control demands has been argued to reflect weak associations between target and cues (Martin & Cheng, 2006; Wagner, Maril, Bjork, & Schacter, 2001).

Additionally, deficits of semantic control in SA patients also extend to an entirely non-verbal domain. For example, Corbett and colleagues (2009) found that performance on a naturalistic object-use task depended on task demands, i.e., patients’ performance was reduced when performing object actions that involved multiple sub-tasks, such as, dual-task conditions, or when a semantically associated distracting object was presented along with the probe. This

provides further evidence that SA patients have damage to an amodal semantic control network (Jefferies & Lambon Ralph, 2006). SA patients are also known to have deficits beyond the semantic domain, i.e., in executive control functioning (Baldo et al., 2005; Jefferies & Lambon Ralph, 2006; Stuss & Alexander, 2000; Wiener, Tabor Connor, & Obler, 2004a). Impaired executive control or problem solving are often associated with frontal lesions (Badre, Hoffman, Cooney, & D'Esposito, 2009; Turken & Swick, 2008; Stuss, 2007). In a study by Baldo et al. (2005), it was found that performance on the Wisconsin Card Sorting Task correlated with picture naming and comprehension (see also Dronkers, Ludy, & Redfern, 1998; Hermer-Vazquez, Spelke, & Katsnelson, 1999; Nelson, Reuter-Lorenz, Persson, Sylvester, & Jonides, 2009; Wiener et al., 2004). Baldo et al. suggested that for complex problem solving, overt language might be required: perseveration errors also correlated with language abilities and further suggested that cognitive switching and flexibility may also depend on language. In a later study by Baldo et al. (2010) it was found that aphasic patients were disproportionately impaired on pattern matching, relative to relational reasoning, and that their language scores correlated with their performance on Raven's Progressive Matrices. However, in a study by Jefferies and Lambon Ralph (2006), these correlations were not found for SD patients, but strong correlations were found between semantic performance and executive control measures, including non-verbal tasks such as picture association matching for SA patients. However, significant correlations do not prove causality, so it could be either that reasoning is impaired by semantic deficits, or that poor semantic control is at least partially underpinned by executive deficits.

Converging evidence for a role of the left inferior frontal gyrus (LIFG) in semantic control

As noted above, patients with semantic aphasia have deficits in the flexible and controlled retrieval of conceptual information and these problems are associated with infarcts in either left inferior frontal cortex, or left temporoparietal cortex (Corbett et al., 2009; Jefferies & Lambon Ralph, 2006; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010). There is much converging evidence from neuroimaging and neurostimulation studies for a role of left inferior frontal cortex, particularly LIFG, in semantic control. One such study by Hoffman et al. (2010) showed reduced comprehension of abstract words without a related cue in both SA patients and participants with inhibitory repetitive transcranial magnetic stimulation (rTMS) to LIFG.

The left lateral inferior prefrontal cortex (LIPFC) is thought to support semantic control processes such as the retrieval, control and/or maintenance of information (Badre & Wagner, 2002, 2007; Fiez, 1997; Jefferies & Lambon Ralph, 2006; Miller & Cohen, 2001; Noonan, Jefferies, Visser, & Ralph, 2013). Moreover, converging evidence has proposed the involvement of the left

inferior frontal gyrus (LIFG) in both lexical and semantic selection (Devlin, Matthews, & Rushworth, 2003; Hirshorn & Thompson-Schill, 2006; Moss et al., 2005; Schnur et al., 2009, 2006, Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2012, 2011). LIFG activity has thus been established during tasks that require controlled access to semantic knowledge (Badre & Wagner, 2007; Buckner, Raichle, & Petersen, 1995), which can result from both high controlled retrieval demands and high selection demands (Badre et al., 2005; Gold, 2006; Badre & Wagner, 2007).

Semantic tasks that are more demanding have been found to activate regions in BA 44, 45, and 47 of LIFG (Desai, Conant, Waldron, & Binder, 2006; Roskies, Fiez, Balota, Raichle, & Petersen, 2001; Ullsperger & von Cramon, 2001). On the other hand, semantic tasks that are less demanding, such as verifying word associations, involve little or no activation in the LIFG (Martin, Wiggs, Ungerleider, & Haxby, 1996; Wise et al., 1991). There are two fundamental ways to increase task demands: (i) by increasing selection demands, i.e., by manipulating an aspect of semantic knowledge that is required for a particular task, for instance, matching the colour of an item activated previously, such as PANTHER with TREACLE, and (ii) by increasing retrieval demands, such as retrieving weak associations (e.g., DENTIST – 'ache'). According to Badre et al. (2005), there are two steps involved in semantic control: (1) the initial controlled retrieval, and (2) post-retrieval selection. While the posterior middle temporal gyrus and the anterior prefrontal cortex (BA 47) are important for the initial retrieval, the posterior prefrontal cortex (i.e., BA 44/45), are involved with post-retrieval selection. Various studies have thus tried to investigate the exact role of the LIFG by differentiating between selection and retrieval. Weakly associated stimuli increase activation of LIFG, as these stimuli pose more demands on controlled retrieval mechanisms, as opposed to strong associative strengths of stimuli that possibly depend more on automatic retrieval processes (Chou, Chen, Wu, & Booth, 2009; Wagner et al., 2001).

The role of LIFG in selecting between competing items has been supported by several studies (Badre et al., 2005; Bedny et al., 2007; Nagel, Schumacher, Goebel, & D'Esposito, 2008; Pisoni, Vernice, Iasevoli, Cattaneo, & Papagno, 2015; Robinson, Shallice, Bozzali, & Cipolotti, 2010; Wagner et al., 2001). In a study by Thompson-Schill and colleagues (1997), LIFG activity increased with greater selection demands, even when the retrieval demands were reduced or held constant (see also Snyder et al., 2010). Evidence for this comes from a goal driven task, where selection was based on information relevant to the task, such as selecting a related item on the basis of its colour (e.g., BLOOD with BEETROOT), which requires retrieving the initial meaning of items before making a selection based on the feature. On the other hand, no post-retrieval selection is required for example when comparing items based on their global properties, such as RAISIN and

PRUNE. Within this experiment, participants were also asked to retrieve an associated action or colour in response to a presented word, such as APPLE, and manipulations of increasing selection demands and reducing retrieval demands were induced by presenting the same item and asking participants to select a different feature. Although the concept had been retrieved already, activation in the LIFG increased, proposing a role of selection demands. Similar results were also presented in a study by Moss et al. (2005) using a picture naming task, requiring automatic retrieval processes, but with the use of competitor priming, which increases selection demands of the task, and subsequent increases were seen in LIFG activation. Further evidence for this comes from tasks with cognitive control paradigms (such as go/no-go, Stroop task or working memory task), and language tasks (such as, resolution of lexical ambiguities, or word generation), both of which reflect high LIFG activation (Novick, Trueswell, & Thompson-Schill, 2010; Thompson-Schill et al., 1997).

SA patients reveal impairments on semantic and executive tasks that are correlated, which would mean that both semantic and executive control tasks share properties. Semantic tasks that are difficult involve regions with domain-general control, such as the dorsal or posterior parts of LIFG. An overlap between these regions of LIFG has indeed been found in fMRI studies that involve both semantic and non-semantic tasks (Duncan & Owen, 2000; Nagel et al., 2008; Wagner et al., 2001). For example, common areas of activation were found in tasks involving a phonological decision (such as, “are there two syllables?”) and a semantic decision (“is it manmade?”; Devlin et al., 2003). As discussed previously, LIFG activity is also associated with language production tasks, when context demands are high, or with increasing semantic or lexical competitors (e.g., Schnur et al., 2006). However, there are implications of its role even beyond language production tasks (Hagoort, 2005; Thompson-Schill, 2003), particularly in semantic memory retrieval tasks (e.g., Badre et al., 2005). Further evidence comes from activation in Broca’s area during action or face recognition tasks (Hamzei et al., 2003; Rajah, Ames, & D’Esposito, 2008), or visual target tasks (e.g., Fink et al., 2006). There is also evidence that the anterior regions of the LIFG are dedicated for semantics. In a study using both non-semantic (e.g., deciding if words or pseudowords were long or short vowel items) and semantic task (e.g., whether words were concrete or abstract), Gold and Buckner (2002) found common areas of activation for semantic and phonological decisions, and stronger activation for semantically controlled decisions. This suggested that regions in the LIFG are dissociable, with posterior LIFG engaged more in phonological control, and anterior portions being involved during semantic decisions (see Poldrack et al., 1999).

Previous accounts have therefore suggested that increasing demands of a semantic task can also increase LIFG activation (Desai et al., 2006; Roskies et al., 2001; Ullsperger & von Cramon, 2001). In line with this, inhibitory TMS delivered to LIFG has also been shown to disrupt tasks with high retrieval and high selection demands (Krieger-Redwood & Jefferies, 2014; Whitney et al., 2012, 2011). Since this top-down control seems to be mediated by LIFG it makes a significant contribution in not only resolving competition but also retrieving relevant aspects of semantic or lexical information (Bedny, McGill, & Thompson-Schill, 2008; Schnur et al., 2009; Thompson-Schill et al., 1997), suggesting that LIFG plays a role in both aspects of semantic control (Raichle et al., 1994; Wise et al., 1991).

In summary, the research reviewed above supports an account of semantic cognition in which the accessibility of conceptual information does not only reflect the structure of knowledge within the semantic store itself (i.e., the fact that weak conceptual representations are harder to retrieve) but instead reflects an interplay between the semantic store (assumed to draw on ATL) and semantic control mechanisms in LIFG. Weak conceptual links can be recovered efficiently through the engagement of LIFG (potentially alongside other brain regions that might also contribute to controlled aspects of semantic cognition), since this brain area is thought to play a critical role in increasing the accessibility of relevant yet weak information through a process of “controlled retrieval” and also “selection” mechanisms that are needed when there is strong competition with the target concept. Building on this component process account of factors affecting the accessibility of conceptual information, the next section considers changes that might occur to semantic accessibility in the context of sustained retrieval of semantically-connected information.

Retrieval-induced changes in semantic access

Refractory impairments in stroke aphasia

Patients with semantic ‘access’ impairments show ‘refractory’ effects (Warrington & Cipolotti, 1996; Warrington & McCarthy, 1983; Warrington & McCarthy, 1987). This describes a pattern of behaviour during a cyclical task, where participants see a target and distractors, which are repeated in cycles so that the target on one trial becomes a distractor on another. After multiple repetitions, performance declines in SA patients: i.e., the patient is no longer able to recognise an item which they correctly identified at the beginning of the block (Cipolotti & Warrington, 1996; Crutch & Warrington, 2008; Forde & Humphreys, 1995, 1997; Gardner et al., 2012; Jefferies et al., 2007; McNeil, Cipolotti, & Warrington, 1994; Schnur et al., 2009; Schnur,

Schwartz, Brecher, & Hodgson, 2006; Warrington & McCarthy, 1987). As performance on one trial does not correlate with performance later on the same trial, this indicates that the item is not degraded but *inaccessible* at certain times (Cipolotti & Warrington, 1996). This has been described as the semantic system entering a 'refractory' state, although the precise mechanisms leading to the decline in performance have been debated. The effect is maximised when items are presented at a fast rate (e.g., with a response-stimulus interval of 0s, instead of 5s, giving the system no time to recover from the previous processing; Campanella, Mondani, Skrap, & Shallice, 2009). It is also stronger within sets of items that are highly semantically related (e.g., when the set of items contains four animals, instead of four objects from different categories), indicating that this mechanism should be localised to the conceptual system.

There have been several accounts put forward to explain 'refractory' effects. One theory proposes that refractory effects arise due to competition amongst the lexical entries that are co-activated as a consequence of their semantic relatedness (Damian, Vigliocco, & Levelt, 2001); as these entries compete for retrieval, selection of the target is thus subsequently delayed (Caramazza, 1997; Humphreys, Riddoch, & Quinlan, 1988; Levelt, Roelofs, & Meyer, 1999). This account potentially provides an explanation of refractory effects in patients with deficits in lexical selection in the context of picture naming (Schnur et al., 2006). However, patients with semantic access deficits show parallel deterioration in their performance on comprehension tasks such as cyclical word-picture matching (Jefferies et al., 2007). Moreover, since the semantic control system is thought to be multimodal – and deficits in semantic aphasia affect verbal semantic tasks plus non-verbal domains such as object use (Corbett et al., 2009) – it follows that refractory effects should extend to non-verbal comprehension tasks. While there was initially strong debate about this hypothesis, with some authors arguing that refractory effects were specific to verbal or auditory comprehension (Crutch & Warrington, 2008; Forde & Humphreys, 1997; Warrington & Crutch, 2004), recent studies have provided evidence that refractory tasks extend to purely non-verbal paradigms, including picture-to-picture matching (Forde & Humphreys, 2007; Gardner et al., 2012). Gardner et al. (2012) tested SA patients and presented items using different modalities; refractory effects were found across verbal (spoken word-picture matching) and visual (picture-picture matching) modalities, in associative matching and cyclic categorical tasks. These multimodal refractory effects in comprehension tasks presented in different modalities can potentially be explained again in terms of the build-up of competition at the conceptual level; for example, according to Jefferies et al. (2007), an external control system selects the correct item appropriately from a set of highly related and strongly activated competitors. Because semantic activation spreads to semantically related items, and does not decay fully between trials due to

the fast presentation rate, all the items in the set become highly activated, and therefore compete for selection along with the target. This build-up of competition increases across repeated cycles, making competition greater towards the end than at the beginning. An alternative account was put forward by Gotts and Plaut (2002), who proposed that successful access to concepts is dependent on a number of neuromodulatory systems, which act to decrease the effects of refractory processes at a physiological level, that operate naturally in the healthy brain. After items are retrieved, they may be suppressed and this suppression may spread to related items, influencing subsequent trials. These accounts may be related in cognitive terms however, since the release of neuromodulators to overcome refractory effects may be dependent on executive control.

Campanella and Shallice (2011) attempted to distinguish these various accounts by reviewing the factors that affected accuracy as a consequence of refractory tasks. Their findings suggested that semantic distance between the target and distractors heavily influenced patients' performance; with a greater distance, the access to the target was easier, and therefore refractory effects were reduced – this finding supports a role for competition in semantic access impairment. The second factor was the presentation rate of the stimuli: a shorter interval between one stimulus and the next impaired performance, while longer intervals between stimuli improved performance. Lastly, they found that refractory effects were also influenced by serial position, i.e., patients had difficulties recognising a stimulus that had been presented several times previously (see also Jefferies et al., 2007). An example of the above factors was seen in the first 'access' patient (V.E.R; Warrington & McCarthy, 1983), who had word comprehension impairments and was strongly affected by presentation rate: a delay of 10 seconds between responses improved her performance significantly. Also, her performance was inconsistent for any presented stimulus from trial to trial, and there was a strong serial position effect, reflecting a decline in performance when a stimulus item was probed the second time. Lastly, she was also influenced by the semantic relatedness of items, such that performance deteriorated for stimulus sets that were closely semantically associated. In a later study by Mirman and Magnuson (2008), it was found that word recognition was facilitated by distant semantic neighbours, whereas word recognition was inhibited with near semantic neighbours. They explained this in terms of an 'attractor dynamics' account, which suggested that facilitation effects of distant neighbours occurred because they create a broader attractor basin, while near neighbours slow the process of recognition as they produce conflicting sub-basins that inhibit performance (Mirman & Magnuson, 2008).

In summary, there has been much debate surrounding the nature of refractory effects, and if they are caused by 'too much inhibition', or 'too much activation'. On one side of the argument, refractory behaviour could be caused by 'spreading inhibition' (Gotts & Plaut, 2002), i.e., due to the temporary inhibition of the closely associated semantic competitors of the item that was produced on the previous trial (Vitkovitch, Rutter, & Read, 2001). On the other hand, 'spreading activation' could also induce refractory behaviour, i.e., following activation of an item, its related features are also activated, and maintain these levels of activation making these items act as potential competitors in the later selection of a related lexical representation (Forde & Humphreys, 1997). In line with this, Belke (2005) proposed an excitatory account, according to which, exaggerated competition between the target and its coordinates in the category can induce a refractory state. For example, in object naming tasks, repeated naming of objects from a homogenous set can cause accumulated activation to build up within the set, between its related concepts and their lexical features and category nodes. Thus, in the retrieval stage, this high level of activation creates competition on a lexical level and also increases the time required for the target to exceed levels of activation in comparison to the sum of activation of its competing lexical nodes, referred to as the 'critical difference threshold' (Wheeldon & Monsell, 1994). However, based on a similar concept, McCarthy & Kartsounis (2000) suggested that inhibitory processes imposed a refractory state on representations, as their patient FAS showed a prolonged refractory state which spread to the lexical nodes related to the target, and made it difficult for FAS to retrieve any appropriate responses (see also Gotts & Plaut, 2002; MacKay, 1982). Both the suppression of semantically-related items (which later become targets) and residual activation of previous targets (which are now distractors) would give rise to a similar effect – difficulty identifying the current target from amongst the field of distractors.

Refractory impairment is associated with damage to LIFG

Neuropsychological studies of brain-damaged patients have identified a relationship between LIFG lesions and semantic interference effects in picture naming (e.g., Biegler, Crowther, & Martin, 2008; McCarthy & Kartsounis, 2000; Wilshire & McCarthy, 2002). Two further group studies by Schnur et al. (2005; 2009) investigated lexical selection using a picture naming paradigm in aphasic patients, and provided evidence that damage to LIFG was related to increasing errors across cycles of naming pictures within a blocked paradigm. Activity in LIFG, assessed by fMRI, was stronger for naming in semantically-related blocks (in which participants repeatedly named sets of items from the same category) as opposed to mixed sets; in addition, the number of errors produced correlated with the degree of the semantic blocking effect in LIFG

(Schnur et al., 2009). These effects were linked by the authors to the importance of LIFG for lexical selection during speech production in the face of competition.

A similar relationship between LIFG damage and increasing impairment has been found in cyclical word-picture matching tasks, assessing comprehension rather than word production (Campanella et al., 2009; Jefferies et al., 2007). Moreover, the same association with LIFG was found for non-verbal comprehension tasks based on picture-picture matching (Gardner et al., 2012; Thompson, Robson, Lambon Ralph, & Jefferies, 2015). These effects were linked to a deficit in semantic control by Gardner et al. (2012), who suggested that impairments on cyclical comprehension tasks can be explained by the inadequate working of the multimodal selection mechanisms supported by left inferior prefrontal cortex, since these are thought to play a crucial role in resolving competition between semantic competitors that might become strongly activated following the repetition of sets of semantically related items. This hypothesis is consistent with broader neuroscientific evidence that LIFG contributes to semantic selection (Kan & Thompson-Schill, 2004; Noonan, Jefferies, Visser, & Ralph, 2013; Thompson-Schill et al., 1998; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, 2003; Wagner, Desmond, Demb, Glover, & Gabrieli, 1997; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2010). Additionally, a lack of propositional speech, which is a primary characteristic of anterior aphasia, has also been linked to a failure in controlled selection demands (Robinson, Blair, & Cipolotti, 1998; Robinson et al., 2005).

Although evidence suggests that damage to LIFG is strongly implicated in the 'refractory' effects described above, other semantic control tasks also require regions beyond LIFG, particularly posterior temporal/inferior parietal areas (posterior middle temporal gyrus and dorsal parts of angular gyrus bordering intraparietal sulcus). These regions can also be damaged in patients who have poor semantic control (Jefferies & Lambon Ralph, 2006; Noonan et al., 2010). Functional neuroimaging studies also show recruitment of a broad network beyond LIFG in task contrasts loading semantic control, including pMTG (Davey et al., 2016; Noonan et al., 2010). It is not yet clear if patients with damage to these posterior regions implicated in semantic control would show mild semantic refractory impairments (e.g., increased response times rather than increases in errors; Jefferies et al., 2007), or if cyclical tasks load on the ability to rapidly implement alternative goals for retrieval (based on the probe identity) and this draws more strongly on LIFG. While both LIFG and pMTG contribute to semantic control broadly defined, they may differ in terms of their engagement by top-down goals and bottom-up recognition of inputs needing control to be employed (Davey et al., 2016).

Fatigue in aphasia

Patients with semantic access deficits present with inconsistent performance and comprehension that declines over time when same items are presented repeatedly, i.e., 'refractory' effects. This decline in performance as a consequence of earlier retrieval could potentially be linked to post-stroke fatigue, since patients with aphasia might experience more difficulty than healthy participants in maintaining goals for semantic retrieval over successive items (e.g., in the course of a conversation). For example, the difficulty of language or conceptual processing might relate to subjective feelings of fatigue in this group. Fatigue is one of the most common consequences of stroke, and it can persist even after patients have substantially recovered (Staub & Bogousslavsky, 2001). Not many studies have tracked the experience of post-stroke fatigue over time; one of the studies showed that since admission to hospital, to a course of six months, and even one year after stroke, the sensation of fatigue increased over time (Schepers, Visser-Meily, Ketelaar, & Lindeman, 2006). There is currently no accepted, valid or reliable definition of post-stroke fatigue, which can be acknowledged by clinicians, patients or researchers. This could perhaps be a consequence of its universal prevalence but subjective or vague definitions, and largely unknown underlying cause, which makes post-stroke fatigue a largely under-treated and under-diagnosed symptom (Lynch et al., 2007). Measurement of fatigue often uses self-estimation scales (Lynch et al., 2007), however it is not clear if patients always have insight into the effects that fatigue might have on their cognitive performance.

One study found that two years after stroke the prevalence of fatigue among patients with no speech impairments was less in magnitude in comparison with patients with speech impairments at admission (Glader, Stegmayr, & Asplund, 2002). However, further relevance of post-stroke fatigue to language deficits is yet to be examined. Discussion of this is important as fatigue plays a detrimental role in both psychological and physical recovery after stroke, and is currently one of the greatest barriers in rehabilitation (Crinion, Holland, Copland, Thompson, & Hillis, 2012; Pedersen, Vinter, & Olsen, 2004; Wade, Hewer, David, & Enderby, 1986).

What factors influence the accessibility of conceptual information in young healthy adults?

In healthy adults, factors influencing the accessibility of knowledge have been examined in multiple disparate literatures, which suggest that retrieval can block access to related information but in different ways: (i) 'Retrieval-induced forgetting' (RIF) – most commonly explored in episodic memory, this work suggests that retrieval necessarily suppresses related information to deal with competition at the point of retrieval. (ii) 'Semantic satiation' – this is

thought to reflect adaptation/habituation, and to occur in the absence of competition. (iii) Psycholinguistic accounts of ‘semantic interference’ – most commonly reported in speech production, this work shows performance declines when semantically-related items are repeated (and often increases in comprehension), but these declines can also be found in some circumstances that could be linked to RIF and/or satiation effects. While there are some similarities with refractory effects in patients with semantic control deficits, there are also some important differences discussed in this section.

Retrieval-induced forgetting

Within episodic memory, retrieval of a specific memory can be impaired by the retrieval of a *related* memory, referred to as ‘retrieval induced forgetting’ (RIF; Anderson et al., 1994). According to this concept, retrieval depends on inhibitory mechanisms to overcome interfering effects from competing memories, which can cause episodic forgetting (for a review see Anderson, 2003; Anderson, Bjork, Bjork, & Jordan, 2000). These mechanisms are thought to suppress the accessibility of competitors, thus increasing the availability of target information (Healey, Campbell, Hasher, & Osher, 2010). RIF effects have been commonly reported in tests of recognition memory (Spitzer & Bäuml, 2007), cued recall tests (Anderson et al., 1994), and implicit memory tests (Veling & van Knippenberg, 2004). However, episodic forgetting has also been reported in studies using semantic knowledge, such that semantic retrieval elicits memory impairments (see Bäuml, 2002; Blaxton & Neely, 1983). Although not many studies have examined this, there is some evidence that RIF effects can also elicit semantic forgetting, as seen in lexical ambiguity resolution (e.g., Simpson & Kang, 1994; see also Gernsbacher, Keysar, Robertson, & Werner, 2001), however, inhibitory effects in most semantic studies have been examined using reaction times, which could either reflect inhibition, or that participants take longer to respond when competing memories are highly activated, as opposed to suppressed (see next section). One study however reported RIF in semantic knowledge based on a word generation task, using ambiguous words and multiple examples from a category (see Johnson & Anderson, 2004), proposing that like episodic recall, semantic retrieval can also affect accessibility of knowledge by the suppression of conceptual distractors. However, the underlying mechanisms of interference effects within semantic domain remain debated and have been further discussed in the next section.

As noted previously, the role of the left prefrontal cortex has been widely associated with controlled retrieval of memory, and also more generally in resolving interference effects (for a review see Fletcher & Henson, 2001; Thompson-Schill et al., 1997). Studies examining neural

activity in healthy participants have indeed implicated the role of frontal activity in RIF. Several fMRI studies have reported that the lateral regions of the prefrontal cortex, in particular the dorsolateral (DLPFC) and the ventrolateral prefrontal cortex (VLPFC), mediate inhibitory control processes that suppress memories at encoding and/or retrieval (Kuhl et al., 2011; Paz-Alonso, Bunge, Anderson, & Ghetti, 2013; Reber et al., 2002; Rizio & Dennis, 2016; Wimber, Alink, Charest, Kriegeskorte, & Anderson, 2015; Wimber, Rutschmann, Greenlee, & Bäuml, 2008; Wylie, Foxe, & Taylor, 2008). Based on connectivity analyses (see Benoit & Anderson, 2012; Gagnepain, Henson, & Anderson, 2014), a top-down modulatory effect of the PFC has been found to reduce activity in the hippocampus, and also in sub-regions of the medial temporal lobe (Anderson et al., 2004; Benoit & Anderson, 2012; Butler & James, 2010; Depue, Curran, & Banich, 2007; Gagnepain et al., 2014; Levy & Anderson, 2012; Paz-Alonso et al., 2013), that subsequently affect the magnitude of forgetting. Studies have similarly shown that the initial involvement of the prefrontal mechanisms can predict forgetting on later recall tests (see Wimber et al., 2015, 2008). These suppression-induced fronto-hippocampal interactions have been reported across various tasks, such as with visual objects (Gagnepain et al., 2014) or words (Benoit & Anderson, 2012; Butler & James, 2010; Levy & Anderson, 2012; Paz-Alonso et al., 2013), suggesting that suppression-induced processes are domain general. Although previous studies have collectively established the role of the lateral PFC in controlling aspects of memory retrieval, particularly memories that participants were instructed to remember/forget either at encoding or retrieval, the neural mechanisms involved in the suppression of semantic representations in the RIF paradigm remain unclear.

Semantic satiation

Within semantic memory, a distinct yet potentially related body of literature on 'semantic satiation' explains how repetition of the same item can lead to a subjective loss of meaning and decline in categorisation accuracy in healthy participants (Balota & Black, 1997; Black, 2004; Black et al., 2013; Kounios, Kotz, & Holcomb, 2000; Pilotti, Antrobus, & Duff, 1997; Smith & Klein, 1990; Tian & Huber, 2010). Repetition of a particular item can either have facilitative effects or inhibitory consequences (Mirman, Britt, & Chen, 2013). Perhaps the most robust example of facilitation is repetition priming, which shows that processing of an item is faster and more accurate on the second presentation than on the first (e.g., Cave & Squire, 1992; Goldinger, 1998; Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991; Ratcliff & McKoon, 1988; Scarborough, Cortese, & Scarborough, 1977). Therefore, it is intriguing that massed exposure to a stimulus can lead to inhibitory consequences (Balota & Black, 1997; Black, 2001). The concept of semantic

satiation refers to the subjective changes or a loss of meaning of a word with repeated and prolonged presentations, such that the repeated stimulus is no longer meaningful (Esposito & Pelton, 1971; Jakobovits & Lambert, 1962; Smith & Klein, 1990). Semantic satiation can dampen the availability of a semantic stimulus (Black, 2004), in the same way that habituation can involuntarily and passively dampen the availability of a perceptual stimulus, and thus, semantic satiation can be viewed as a semantic analogue to habituation.

Investigations into the satiation effect have been carried out using a number of different measures, including word association and introspection tasks (Esposito & Pelton, 1971). These effects have been reported on tasks requiring semantic access, such as semantic priming tasks, which involve repeated presentations of a prime word, (e.g., 'dog'), followed by a relatedness judgement task based on a prime-target pair (e.g., 'dog' – 'cat'). Judgements on this paradigm are faster for responses to related prime pairs in comparison to unrelated pairs (Meyer & Schvaneveldt, 1971). Semantic satiation is measured by the difference in response times between the related and unrelated pairs over time – this is shown to decrease significantly with prime repetitions, as the benefits of semantic priming are reduced (Balota & Black, 1997; Black, 2001; Black et al., 2013; Kounios et al., 2000; Pilotti et al., 1997; Pilotti & Khurshid, 2004). Semantic satiety effects are also seen in reduced accuracy following prime repetitions (Balota & Black, 1997; Black et al., 2013). These effects are not observed on lexical decision tasks (Cohene, Smith, & Klein, 1978; Neely, 1977; Smith, 1984), perhaps because these are often made without the need to access semantic information (Black et al., 2013; Smith, 1984). Therefore, semantic satiation effects require semantic access as a necessary condition.

Moreover, according to Kanungo & Lambert (1963), following the constant repetition of a word, there is a decline in the number of words that a participant can retrieve that are related to that word, therefore suggesting a kind of cognitive 'fatigue' of thinking. Additionally, the associates of the repeated word that are in fact retrieved or named do not tend to be the typically strong associates of that word, but rather the less common associates (Smith & Raygor, 1956). In another study it was found that repeating an associated word for a minute had also affected the time needed to decide if the subsequent pairs of words were synonyms or not (Fillenbaum & Jones, 1965). Together these studies suggest that any inhibitory effects produced through repeated activation are not only restricted to the semantic unit involved but are also likely to spread to units that are related, or are more commonly associated with the word. Satiation effects are thus conceptualised within a spreading activation framework, i.e., following the first access to the repeated word, its underlying conceptual representation are also activated and this

activation then spreads to related areas within the memory network (Balota & Black, 1997; Collins & Loftus, 1975; Neely, 1977a). According to a proposal by Smith & Klein (1990), with repeated exposure these conceptual nodes become fatigued, which reflects a similar process by which a neural ensemble becomes fatigued following repeated stimulation. A number of fMRI and PET studies have observed a similar reduction in neural activity with repetition of stimulus, causing synaptic depression (e.g., Buchel, Coull, & Friston, 1999; Buckner et al., 1995; Schacter, Alpert, Savage, Rauch, & Albert, 1996; Wagner et al., 2000), and synapses that have been activated in the processing of a recent stimulus are the ones that are most likely to be depressed following repetition (Gotts & Plaut, 2002).

Habituation has been argued to build up in the lexical-semantic links, but effects that cross modalities suggest a genuinely conceptual-level mechanism. Thus, further investigation into understanding satiation effects comes from multimodal studies. Pilotti and Khurshid (2004) used a multimodal presentation approach, finding evidence of a semantic satiety effect after combined visual word and auditory word presentation. Semantic satiety effects have also been found when pictures of faces (Lewis & Ellis, 2000) and pictures of category exemplars (Takashi, 2007) were repeatedly presented. Though non-significant these effects have also been reported in response to repeatedly presented photographs (Jakobovits, Lambert, & Un, 1964). This suggests that semantic satiety might be a phenomenon that occurs for all concepts and is not restricted to words.

In summary, research on 'semantic satiation' has shown that categorisation and semantic retrieval declines as a consequence of previous exposure and retrieval. In this way, semantic satiation effects appear to be a semantic analogue of the 'retrieval-induced forgetting effects' in episodic memory, discussed above. The mechanism that might underlie semantic satiation is debated and has been described as a form of passive habituation; however, drawing on the literature on retrieval-induced forgetting, it is also possible that this effect occurs as a natural consequence of controlling the competition that occurs at initial retrieval – i.e., in order to recover a specific conceptual representation, other semantically-related competitors might be suppressed and this affects their subsequent availability. In addition, several aspects of semantic satiation in healthy participants resemble semantic refractory effects in people with aphasia – for example, in both sets of studies, close semantic associates show a greater decline in retrieval. There has also been substantial debate in both literatures about whether the effects arise at the level of lexical representations or lexical-semantic links, or instead at the level of conceptual representations. In both cases, demonstrations of retrieval-related declines in performance, in

entirely non-verbal paradigms suggests that the effects are conceptual in origin, although this warrants further investigation. Despite these similarities, however, there are also some important differences: most notably, semantic satiation paradigms tend to involve extended presentation durations, while refractory effects are highly sensitive to response-stimulus interval – they are only observed when the delay between successive trials is minimised.

Psycholinguistic models and cumulative learning accounts

Psycholinguistic studies, examining changes in language performance with repetition of items or semantically-related stimuli, have observed similar effects – i.e., decreasing lexical-semantic retrieval with ongoing processing: these effects are largely seen in picture naming (Damian et al., 2001; Riley, McMahon, & de Zubicaray, 2015), and have also been shown to affect comprehension in some studies (Campanella & Shallice, 2011; Harvey & Schnur, 2016; Wei & Schnur, 2015). There is a long-running debate about whether the interference effects arise at the lexical level (Crutch & Warrington, 2003; Damian et al., 2001), within lexical-semantic links, or at the conceptual level (Belke, 2013; Gardner et al., 2012; Wei & Schnur, 2015). The underlying mechanisms are also unclear, with some accounts proposing competition between currently-activated representations (Belke, Meyer, & Damian, 2005; Oppenheim, Dell, & Schwartz, 2010; Schnur, Schwartz, Brecher, & Hodgson, 2006), and other researchers noting that the effects are long-lasting, and are therefore more likely to reflect weight changes between associated items (Howard et al., 2006; Oppenheim et al., 2010).

One way of accounting for these effects within psycholinguistic models is to envisage that during the processing of one item, competitors are co-activated by virtue of the links between concepts and words. For example, on encountering the word CAT, the features of this animal are activated, and this in turn activates words with similar features such as DOG. This can then induce substantial *semantic interference* (Abdel Rahman & Melinger, 2011; Belke, 2008; Belke et al., 2005; Damian et al., 2001; Howard, Nickels, Coltheart, & Cole-Virtue, 2006; Kroll & Stewart, 1994; Navarrete, Mahon, & Caramazza, 2010). This could account for increasing latencies in cyclical picture naming studies when sets of semantically-related items are named repeatedly (Kroll & Stewart, 1994; Vitkovitch & Humphreys, 1991). Moreover, performance on this paradigm is sensitive to semantic variables, such as the strength of the association between the items, suggesting that activation at the conceptual level underpins this effect (Abdel Rahman & Melinger, 2011). Healthy participants typically do not show declining performance on cyclical word-picture or picture-picture matching tasks (Damian et al., 2001; Riley, McMahon, & de Zubicaray, 2015), and thus do not resemble patients with LIFG lesions (see above). This suggests

that semantic interference effects in picture naming may readily accumulate even when the contribution of LIFG is intact, while semantic control exerted by LIFG may allow participants to overcome interference in simple comprehension tasks such as word-picture matching even when competitors are conceivably strengthened on later cycles.

A “continuous picture naming” paradigm can also elicit declining performance when conceptually-related items are presented in succession (i.e., two animals), even without the repetition of individual items (Belke & Stielow, 2013; Belke, 2013; Howard et al., 2006; Kleinman, 2013; Navarrete, Mahon, & Caramazza, 2010; Oppenheim et al., 2010; Runnqvist, Strijkers, Alario, & Costa, 2012; Schnur, 2014). For example, in the sequence GOAT, CAR, TOMATO, TRUCK, HORSE, the naming time for HORSE would be slower than that for GOAT due to their conceptual overlap, and this effect is found even at long ‘lags’ with many unrelated intervening items. Since this effect appears to be relatively long-term (cf. Wheeldon & Monsell, 1994), it may reflect cumulative weight changes, as opposed to on-going activation. On the basis of these long-term interference effects from the continuous naming paradigm, Howard et al. (2006) suggested that three mechanisms are necessary for interference effects in naming tasks. Firstly, the effect arises with *shared activation*. Findings from blocked cyclic naming tasks have shown that interference effects are stronger for more closely related items rather than distant ones (Vigliocco, Vinson, Damian, & Levelt, 2002), thus it is essential that the items share semantic features, which can promote increased activation of lexical competitors. The second mechanism is *lexical selection by competition*. Some studies have suggested that this arises following semantic access and before phonological access. For example, in a non-verbal semantic judgement task, presentation of pictures in a blocked cyclic paradigm did not produce semantic blocking effects (Damian et al., 2001). Thus, any competition occurring in stages preceding lexical access was not sufficient enough to induce interference effects. This was further supported by a bilingual continuous paradigm experiment, which indicated that interference effects accumulated for each language independently, suggesting that these competitive selection processes are language specific, and occur post-semantic access (Castro, Strijkers, Costa, Costa, & Alario, 2008).

Repetition priming is the last mechanism required for cumulative semantic interference (Howard et al., 2006). Previous retrieval of a word can prime its future retrieval, and this can make the word a stronger competitor when associated words need to be retrieved in later trials. The effects of priming can be considered in two ways – ‘temporary’ or ‘persistent’. Priming can have temporary effects on activation levels carried over from previous trials: for example, selection of the word SALT might temporarily suppress PEPPER, making it harder to access PEPPER for

a short while. On the other hand, persistent accounts of priming suggest comparatively permanent changes to the accessibility of the word (e.g., Damian & Als, 2005; Howard et al., 2006; Schnur et al., 2006), and these accounts may be needed to explain semantic interference effects in the continuous paradigm over relatively long lags between semantically-related trials.

A related long-term interference mechanism based on *incremental learning* was proposed by Oppenheim (Oppenheim et al., 2010). This account suggests that rather than changes in the activation levels, each retrieval episode results in changes to connection weights (for example, between semantic and lexical representations, in the context of picture naming). By this view, the naming of DOG increases the weight between animal features and this lexical representation, and weakens the connection between the animal category and other semantically-related lexical forms, such as CAT. In this way, learning is thought to continuously adjust the cognitive system with regards to the task at hand (e.g., Gupta & Cohen, 2002). One of the essential properties of these incremental learning accounts is that interference builds up incrementally as a consequence of experiences that are relevant to the task (e.g., naming pictures that are semantically related). For example, performing a non-linguistic task and naming unrelated items in between naming DOG and GOAT did not disrupt blocking effects (Damian & Als, 2005). Thus, semantic interference effects in naming can arise as a direct consequence of retrieval that renders related items less accessible (see also Anderson, Bjork, Bjork, & Jordan, 2000, for a related phenomenon in memory).

While the above accounts predominantly stem from word production tasks, several recent studies have used the continuous paradigm without item repetition to examine categorisation as opposed to picture naming. In sharp contrast to the results discussed above, these studies observed cumulative *facilitation* as opposed to inhibition (Belke, 2013; Riley et al., 2015). Nevertheless, as mentioned previously, under some circumstances healthy controls can show *declining categorisation* with repetition (Harvey & Schnur, 2015), and thus resemble patients with semantic access impairment. This pattern was observed in cyclical matching to a deadline when there were repeated presentations of the same target plus minimal delays between trials (Campanella & Shallice, 2011): these circumstances potentially create competition between the current target and previous targets (which have become distractors), with little time to resolve this competition or to recover from previous processing. In addition, Wei and Schnur (2015) reported semantic interference in a picture matching task, when the same response options were repeatedly used to probe associations with either related or unrelated concepts; in this study, there was initial facilitation (when semantically-related items were repeated at short

lags; perhaps reflecting faster visual recognition for the probe when immediately following a related item), followed by longer-lasting inhibition (when related trials occurred at longer lags, perhaps reflecting response interference when a similar probe had led to a different decision on a previous trial). However, these studies still involved cyclic presentation of items to influence retrieval of semantically related concepts, and it is thus yet to be established what mechanisms underlie retrieval of information or declining comprehension of semantic stimuli without repetition. This gap in the literature is directly addressed by the work in this thesis.

In summary, the literature reviewed above suggests that healthy participants can show retrieval-induced deficits in semantic retrieval, similar to aphasia patients with control/access impairment. However, while patients show declines in simple word-picture matching tasks when sets of semantically-related items are repeated, healthy participants typically show repetition priming (i.e., facilitation) in the same paradigm. This might be because they have intact semantic control processes in LIFG and this allows them to flexibly update the current goal (i.e., the required target) and exert a top-down influence on the balance of excitation and inhibition of targets (ex-distracters) and distracters (ex-targets) as they perform successive trials. Nevertheless, healthy participants do show some similar effects in continuous picture naming paradigms (perhaps because producing a picture name requires more control over retrieval than recognising a picture, or alternatively, more suppression of the distracters to allow the target to emerge) and in semantic satiation experiments. In contrast to the patient work, where effects tend to be relatively short-lived suggesting a deficit in resolving on-going competition at the point of retrieval, the effects in healthy subjects tend to have an extended temporal duration – i.e., slow presentation times or effects over long lags between semantically-related items. These effects might relate to longer-term changes in the accessibility of information, as opposed to competitive selection processes.

Influence of ageing on the accessibility of knowledge

Most work on semantic satiation and semantic blocking effects in language retrieval has examined younger adults as participants. An important question, especially given the comparisons that have been drawn between these studies and patients with semantic control/access deficits (who tend to be older), is how are these processes affected in healthy ageing. Older adults continue to acquire conceptual information over the lifespan, and tests of semantic knowledge do not show the marked age-related declines seen for episodic and working memory (Cabeza et al., 2004; Haut, Chen, & Edwards, 1999; Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000). However, since semantic cognition is thought to emerge from the interaction of multiple

neurocognitive components, including the conceptual store in the anterior temporal lobes (ATL) and control processes that shape semantic retrieval in left prefrontal cortex (Jefferies, 2013; Noonan et al., 2013), some aspects of semantic cognition may show greater age-related cognitive decline than others. In particular, the *retrieval* of semantic information may be more vulnerable in ageing than the retention of knowledge itself. Older adults are known to take longer to retrieve information from memory and this slowing might reflect a reduced spread of activity through semantic representations. Recent neuroimaging studies have examined the neural basis of these reductions in memory based on age. Results have indeed reported reduced activation in areas supporting memory, such as the medial temporal lobe and the prefrontal cortex in older compared to younger adults (Grady et al., 1995; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Stebbins et al., 2002). Some of these experiments have also reported more prefrontal activity in older adults than in younger adults during memory tasks, particularly during retrieval (Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, Bernstein, Beig, & Siegenthaler, 2002; Gutchess et al., 2005; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Madden et al., 1999; Morcom, Good, Frackowiak, & Rugg, 2003; Öztekin, Güngör, & Badre, 2012; Rosen et al., 2002)

According to the frontal lobe theory of ageing, changes in cognition occur due to structural and neurochemical changes in the frontal lobes in older adults (Maccotta & Buckner, 2004; Raz et al., 1997; West, 1996). For example, performance on clinical tasks of executive functioning, such as the Trail Making test, and the Wisconsin Card Sorting Test, has been found to deteriorate with age (Fristoe, Salthouse, & Woodard, 1997; Libon et al., 1994). Evidence also suggests that age-related deficits in performance do not result from a uniform frontal-lobe decline; for example, the dorsolateral prefrontal regions are more sensitive to ageing than the ventromedial prefrontal regions (MacPherson, Phillips, & Della Sala, 2002). Recent findings have similarly demonstrated declines with ageing on tasks requiring greater executive control that are subserved by dorsolateral regions (Baciu et al., 2016; Cappell, Gmeindl, & Reuter-Lorenz, 2010; Grady, 1998; Johnson, Mitchell, Raye, & Greene, 1993; Reuter-Lorenz & Lustig, 2005; Schacter, Kaszniak, Kihlstrom, & Valdiserri, 1991; Schneider-Garces et al., 2010; West, 1996). There is further evidence that the reduced activity in frontal regions (Campbell, Grady, Ng, & Hasher, 2012; Schmitz, Cheng, & De Rosa, 2010) affects top-down modulation, which can subsequently weaken controlled retrieval processes (Gazzaley, Cooney, Rissman, & D'Esposito, 2005) supporting selection amongst competing alternatives (e.g., Fleischman & Gabrieli, 1998). These deficits in controlled retrieval have been established using verbal fluency, object naming and semantic categorisation tasks (e.g., Baciu et al., 2016). There is also evidence that older adults are slower in multiple object naming but not in single object naming relative to younger adults, in a

blocked naming paradigm (Belke & Meyer, 2007), suggesting sensitivity to competition effects, and that older adults can be vulnerable to semantic interference effects.

In addition, studies have shown that the progressive loss of frontal activity also affects inhibitory mechanisms, particularly on the influence of irrelevant responses or material (Garavan, Ross, Li, & Stein, 2000), i.e., older adults are less able to suppress irrelevant or distracting information (Lustig, Hasher, & Zacks, 2007). Similarly, studies on regions that index 'default-mode' activity, i.e., when people attend to an internal based focus rather to an external task focus (Gusnard & Raichle, 2001; Raichle et al., 2001), have provided further evidence that ageing can impact decreased inhibition or the capacity to appropriately engage attention. Activity in default-mode regions has been shown to decrease, relative to rest periods, in both auditory tasks (Alain, Arnott, Hevenor, Graham, & Grady, 2001) and visual tasks (Haxby et al., 1994; Shulman et al., 1997). Several studies have reported that default-mode activity in healthy older adults during task performance is not reduced to the same extent as seen in younger adults (Greicius et al., 2004; Lustig et al., 2003).

While the above studies account for age related changes that could potentially affect cognitive functioning, some work has suggested that age has a more direct impact on memory (e.g., Salthouse & Ferrer-Caja, 2003). Some of the earlier priming studies examined whether older adults would show semantic priming effects, and found consistent priming effects for older adults, but with much longer response times in comparison to younger adults (e.g., Cerella & Fozard, 1984; Howard, McAndrews, & Lasaga, 1981; Madden, Pierce, & Allen, 1992). Some studies also varied the stimulus onset asynchrony (SOA), or the interval between the onsets of the prime and target, to examine the speed of semantic activation (i.e., if activation spreads from the prime to the target to cause priming effects depending on the SOA). Mixed results have been produced from these studies, with some indicating an equivalent rate of activation spread (e.g., Balota & Duchek, 1988; Burke, White, & Diaz, 1987; Madden et al., 1992), while others have indicated a slowing in the rate of activation with age (e.g., Howard, Shaw, & Heisey, 1986). Results from semantic priming studies further suggest that ageing affects activation, i.e., automatic processes, in addition to controlled process (see also Balota & Duchek, 1988; Mudar et al., 2015).

However, some of the more recent studies have reported that lower levels of control enable older adults to encode more information compared to younger adults (Campbell, Hasher, & Thomas, 2010; see also Rowe, Valderrama, Hasher, & Lenartowicz, 2006), and this can potentially benefit (or disrupt) performance based on task demands. For example, older adults showed increased priming effects of distractors than younger adults, and this benefitted their

later performance on the task, i.e., older adults were able to use previously-distracting information from previous trials that younger adults had inhibited (Amer & Hasher, 2014; Biss, Ngo, Hasher, Campbell, & Rowe, 2013). Together, these studies suggest that age-related reductions in activation can slow retrieval from memory, and negatively affect performance on goal-based tasks, such as tasks requiring resolution of interference effects; lower levels of control on the other hand can benefit performance on tasks requiring less inhibition, or tasks that require access to previously encountered information (e.g., Amer & Hasher, 2014; Campbell et al., 2010), and thus could also benefit performance by reducing RIF (e.g., Anderson & Bell, 2001). Based on a recent meta-analysis, RIF effects were found to be related to the age of the control group (see Murayama, Miyatsu, Buchli, & Storm, 2014), with older participants being less affected than younger participants and similarly participants over 75 years being less influenced by RIF than participants between 60-75 years (Aslan & Bäuml, 2012). However, the implications of these effects are yet to be determined within semantic memory.

Transcranial direct current stimulation (tDCS)

Given that LIFG plays an important role in semantic control (e.g., Noonan et al., 2013), and in overcoming retrieval-induced decreases in categorisation, at least in patients with aphasia and LIFG lesions (see above), the application of anodal direct current stimulation to this region might be expected to reduce this effect. This method could conceivably be one way of improving retrieval in populations who might have greater difficulty, for example in the context of ageing or aphasia. Transcranial direct current stimulation (tDCS) has been used to enhance brain excitability in the human language network in previous studies (Fridriksson, Richardson, Baker, & Rorden, 2011; Hesse et al., 2007). tDCS delivers a weak polarising electric current to the cortex, via a pair of electrodes, and depending on the polarity of the current used, brain excitability can either be increased, using anodal tDCS or decreased by cathodal stimulation (Liebetanz, Nitsche, Tergau, & Paulus, 2002; Nitsche & Paulus, 2000). Hence, tDCS does not necessarily 'stimulate' neurons but modifies the ongoing activity within regions (M. a Nitsche & Paulus, 2000). The exact mechanisms through which brain activity can be modulated using tDCS are yet to be understood, however, these mechanisms have been categorised into synaptic effects (i.e., alterations in the strength of synaptic transmission), and non-synaptic effects (i.e., changes in resting membrane potential of pre- and post-synaptic neurons; Brunoni et al., 2012; Stagg & Nitsche, 2011). The effects during stimulation reflect modulation of the resting membrane potential, while the effects post-stimulation have been shown to last some time and can be explained by multiple mechanisms, such as the induction of long-term potentiation and depression (Liebetanz et al.,

2002; Nitsche et al., 2003). Pharmacological studies have further characterised the long lasting effects of stimulation as a consequence of changes in synaptic strength through alterations of the levels of the GABA neurotransmitter and the functioning of NMDA receptors (Stagg & Nitsche, 2011). tDCS is also thought to affect protein synthesis (Titushkin & Cho, 2009) and levels of brain oxygenation (Merzagora et al., 2010). The effects of tDCS with regards to changes in task performance have been reported to last as long as six to twelve months post-intervention from repeated stimulation combined with training (Cohen Kadosh, Soskic, Iuculano, Kanai, & Walsh, 2010; Dockery, Hueckel-Weng, Birbaumer, & Plewnia, 2009; Reis et al., 2009). tDCS is considered to be a relatively painless and safe method in comparison with TMS by participants, there are also fewer artefacts with this technique, such as muscle twitching or acoustic noise, and is therefore well suited for clinical applications and also sham-controlled or double-blind studies (Cattaneo, Pisoni, & Papagno, 2011).

Depending on the site of stimulation, neural modulation using tDCS can subsequently influence related cognitive functions (Hone-Blanchet, Edden, & Fecteau, 2016; Hunter et al., 2015). Previous studies have found that anodal tDCS aids cognitive functions, such as planning (Dockery et al., 2009), working memory (Boggio et al., 2006; Fregni et al., 2005), and learning (Kincses, Antal, Nitsche, Bártfai, & Paulus, 2004). In the domain of language, studies with healthy participants have shown that anodal tDCS over LIFG facilitates grammar learning (de Vries, Barth, & Maiworm, 2010), picture naming (Fertonani, Rosini, Cotelli, Rossini, & Miniussi, 2010; Henseler, Mädebach, Kotz, & Jescheniak, 2013; Holland et al., 2011) and verbal fluency (Cattaneo, Pisoni, & Papagno, 2011; Iyer et al., 2005; Penolazzi, Pastore, & Mondini, 2013; but see Vannorsdall et al., 2016). Additionally, anodal tDCS over language areas has also shown to play a role in the recovery of language functions in aphasic participants (see Monti et al., 2013 for reviews; Fiori et al., 2011; Fridriksson, Richardson, Baker, & Rorden, 2011; Marangolo et al., 2011). Most studies on aphasia have been dedicated to language production tasks (Devlin & Watkins, 2007), and preliminary findings have shown that naming performance post-treatment was facilitated using anodal tDCS over the lesioned left hemisphere (Baker, Rorden, & Fridriksson, 2010; Fiori et al., 2011; Fridriksson et al., 2009; Metzuyan-Gorlick & Mashal, 2016).

Relatively few studies have examined comprehension as opposed to language production. However, anodal stimulation to LIFG has been shown to positively affect the categorisation of familiar items, and improved the selection of low-dimensional items or items weakly associated with a category (Lupyan, Mirman, Hamilton, & Thompson-Schill, 2012). Participants were also faster at deciding if a particular stimulus was coherent or incoherent (Cohen-Maximov, Avirame,

Flöel, & Lavidor, 2015), and anodal stimulation to this region facilitated contextual selection and controlled semantic retrieval in a semantic judgement task with lexical ambiguous words (see Ihara, Takanori, & Soshi, 2014). Further evidence comes from enhanced performance on idiom comprehension (see Sela, Ivry, & Lavidor, 2012) and complex verbal problem solving on the remote associates task (RAT), which requires participants to suppress dominant associations (Cerruti & Schlaug, 2009; see also Metuki, Sela, & Lavidor, 2012). Anodal stimulation of LIFG also facilitated relatedness judgements for gestures accompanying language (Cohen-Maximov et al., 2015; Schülke & Straube, 2016), suggesting that these effects are not restricted to verbal stimuli.

Stimulation of the left prefrontal cortex has also shown decreased semantic interference effects in healthy participants, within the blocked picture naming paradigm. The effects of stimulation were observed in naming latencies: the classic finding of slower responses over time, following repeated retrieval of the names of semantically-related concepts presented cyclically within small blocks, was attenuated with tDCS (Meinzer, Yetim, McMahon, & de Zubicaray, 2016; Pisoni, Papagno, & Cattaneo, 2012). Similar findings were also revealed in a study combining tDCS and EEG to examine the behavioural and neurophysiological correlates of stimulation, both during and after tDCS (Wirth et al., 2011). Results showed an increase in prefrontal inhibitory functions following anodal tDCS over the left dorsolateral prefrontal cortex, during a blocked naming paradigm. The after effects of anodal stimulation were detected in the delta band activity, a marker of neural inhibition (Spironelli & Angrilli, 2009), which subsequently reduced the semantic interference effect. Furthermore, modulating LIFG activity with anodal tDCS also enhanced responses within homogenous lists (Schnur et al., 2009). Findings have also shown greater verb naming improvements with the use of excitatory stimulation to Broca's area and the surrounding frontal region (i.e. left dorsolateral frontal cortex), along with intensive language training (Marangolo et al., 2013). Finally, stimulation of the left prefrontal cortex has been reported in studies using paradigms requiring higher control levels, for example, generating words that begin with particular letters (Hirshorn & Thompson-Schill, 2006; Iyer et al., 2005), and generating words from specific categories (Chrysikou et al., 2013; Cohen-Maximov et al., 2015; Lupyan et al., 2012). Meinzer et al. (2012) showed that anodal stimulation of LIFG improved lexical retrieval and reduced accompanying activation of LIFG, and also increased the connectivity of this region with other brain areas underlying the language network. This could possibly reflect strengthening of top-down control processes following LIFG stimulation. Similarly, these effects have found to benefit older adults, in that anodal stimulation to LIFG modulated changes in connectivity and improved performance in older adults up to the level of younger adults in a word generation task (Meinzer, Lindenbergh, Antonenko, Flaisch, & Flöel, 2013).

These findings taken together suggest that anodal tDCS to LIFG strengthens language retrieval and comprehension; these effects may also be strongest in experimental conditions in which there are substantial demands on semantic control. These effects could result from stronger top-down constraints within LIFG allowing the retrieval of conceptual information to be shaped in line with current task demands more efficiently.

Research themes

Theme 1: Retrieval-dependent declines in semantic retrieval – effects of stimuli and task

Previous studies have reported declining comprehension and semantic access following massed repetition of semantically-related stimuli: patients with semantic aphasia show '*refractory effects*' in cyclical word-picture matching tasks (Jefferies et al., 2007; Warrington & McCarthy, 1983); healthy subjects show similar effects in cyclical picture naming (Belke et al., 2005; Damian et al., 2001; Harvey & Schnur, 2016; Vitkovitch & Humphreys, 1991); healthy participants also show '*semantic satiation*' following prolonged repetition of words, causing a subjective loss of meaning (Jakobovits & Lambert, 1962; Smith & Klein, 1990). In all of these paradigms, stimuli are repeated en masse. Similar declines in picture naming are seen in a '*continuous paradigm*', in which items are not repeated: healthy participants show slower naming when multiple pictures are presented from the same category (Howard et al., 2006; Schnur, 2014). Moreover, the ability to retrieve semantic information in a free-association task is reduced by earlier generation of associated knowledge (Johnson & Anderson, 2004). Nevertheless, demonstrations of declining comprehension and categorisation (i.e., in the absence of generation or naming) thus far have utilised repeated presentations of the same items (either as targets or as distracters; Campanella & Shallice, 2011; Harvey & Schnur, 2015; Wei & Schnur, 2015) – it is unclear if the same effects would emerge in the absence of item repetition (especially since research using the continuous paradigm has found *facilitation* in the absence of item repetition; Belke, 2013; Riley et al., 2015).

The thesis work examined if comprehension and categorisation of information would deteriorate over time in the absence of item repetition. A paced serial semantic task (PSST) was used, in which participants monitored a stream of inputs and pressed a button every time they detected a target that matched a particular category. Neither targets nor distracters were repeated – therefore, the task resembled a continuous naming paradigm but required the comprehension and categorisation of meaningful inputs, rather than the production of speech. This task assessed the ability of participants to sustain semantic processing over time: both *within* categories – by examining whether comprehension deteriorated over the course of each category

as more related targets were presented, and *between* categories – by quantifying changes in performance across the experiment, as participants became generally fatigued.

The PSST paradigm allowed for the manipulation of factors linked to both semantic representations themselves – such as strength of association, which should influence the spread of activation to related concepts – and factors linked to control processes that are thought to play a critical role in focussing retrieval on currently-relevant knowledge in the face of strong distractors or weak targets – such as conditions of divided vs. undivided attention. In this way, the task maps onto contemporary accounts of semantic processing, which envisage amodal concepts that interact with control processes to support context- and task-appropriate semantic retrieval (Lambon Ralph, Jefferies, Patterson, & Rogers, 2016). If declining comprehension on the PSST reflects difficulty retrieving relevant information in the face of competition from previously activated but now irrelevant knowledge (e.g., if it is more difficult to decide that “rug” is connected to the category PICNIC when “sunshine” has already been linked to this category because “rug” and “sunshine” share few features), this declining comprehension might be expected to be greater for weakly-associated items (e.g., when the target is “wasp” as opposed to “sandwich”). In other words, in a “too much activation” account, weak targets should have greater difficulty in a categorisation task, because they are more vulnerable to competition (Belke et al., 2005). In contrast, if the declines in comprehension follow from the suppression of other associated knowledge during earlier decisions, it might be expected that the effect would be stronger for highly-associated targets, since the strongest associates would need to be suppressed most strongly to allow other targets to be categorised efficiently (Navarrete, Prato, & Mahon, 2012; Vigliocco et al., 2002). In a similar way, the literature on semantic satiation shows stronger detrimental effects of repetition for strong vs. weak associates (Balota & Black, 1997).

In addition to thematic categories (e.g., PICNIC), taxonomic categories were presented, where target items shared common features (e.g., four wheels, for the category VEHICLES). In addition, a version of the PSST based on a single feature, such as colour (e.g., ‘post box’, ‘tomato’ and ‘Santa’ for the category RED), was developed. The targets in these categories were not globally related and shared few (if any) features, except for the feature specified in the instructions. The contrast between these experiments is informative about the underlying mechanisms. If within-category decline in categorisation reflects unconstrained spreading activation within the semantic system that interferes with the categorisation of incoming items (irrespective of whether this spreading activation concept leads to ongoing competition or longer-term suppression), then this effect would be expected for targets with strong featural overlap (e.g., VEHICLES – ‘car’, ‘bus’,

'truck'), but potentially not the single feature task, where successive targets were unrelated. In contrast, if the categorisation of one target suppresses other representations with goal-relevant features, the effect would extend across all of these different tasks.

Previous research has also found declining performance in cyclical word-picture matching paradigms with fast but not slow presentation speeds, perhaps because rapid presentation allows a build-up of competition from previously-presented semantically-related items (Campanella & Shallice, 2011). In contrast, satiation effects occur when inputs are presented for long durations (Smith, 1984). It might be that slow presentation speeds can elicit habituation or adaptation effects within semantic representations, while fast speeds provide insufficient time for competition to be resolved. Therefore, performance in Chapter 2 was contrasted at a relatively fast speed of presentation (1.1s) and a slower speed (2s), to establish whether this manipulation would alter the extent to which semantic categorisation declined in the PSST paradigm.

Another factor considered in this thesis was whether the systematic decline in the meaning of an item could occur in a manner that is independent of a specific input modality. Declining performance in the cyclical matching paradigm in patients with aphasia has largely been documented using verbal comprehension tasks – i.e., word-picture matching (Cipolotti & Warrington, 1996; Jefferies et al., 2007; Warrington & McCarthy, 1983). It has been suggested that this effect may be exclusive to auditory or verbal materials (Crutch & Warrington, 2008; Warrington & Crutch, 2004). Similarly, in healthy participants, declining performance on cyclical paradigms has been linked to lexical competition during speech production (rather than conceptual retrieval) (e.g., Belke et al., 2005; Harvey & Schnur, 2015; Howard et al., 2006), while in the satiation literature, it has been suggested that declining comprehension comes about due to adaptation of orthographic-to-semantic links (Tian & Huber, 2010) – consequently, these effects of repetition may be restricted to the verbal domain. Nevertheless, SA patients show declining performance across cycles for both word-picture and picture-picture matching tasks (Forde & Humphreys, 2007; Gardner et al., 2012), suggesting that semantic access deficits can occur at an amodal conceptual level. This is consistent with the proposal that semantic cognition draws on amodal representations and control processes that operate across modalities. Decline in performance was assessed for word targets, picture targets and an interleaved condition in which related items were presented as both words and pictures on different trials. If the decline in performance arises at a conceptual level, this effect should not be diminished for the interleaved condition. Additionally, participants were asked to make a response on each trial (pressing one of two buttons to indicate if the item was a member of the category, or not), and there were equal

numbers of targets and distractors. This two alternative-forced-choice (2AFC) design would minimise the effects of response bias.

Theme 2: Effects of semantic control capacity on retrieval-dependent declines in semantic retrieval

Increasing competition across a series of related trials or suppression of items that are later targets are both likely to increase the requirement for semantic control – both selection/inhibition mechanisms that can resolve competition, and “controlled retrieval” processes that allow the promotion of weak and previously-suppressed information that is now relevant (cf. Badre et al., 2005). Consequently, retrieval-induced decline in comprehension might increase in populations or circumstances that reduce the capacity to employ semantic control.

The thesis includes an experiment with healthy participants in which the capacity to apply top-down constraint to semantic retrieval was disrupted through the use of a secondary task to divide attention. Under these circumstances, the requirement to do two tasks at once might have a particularly detrimental effect on comprehension towards the end of each category, when performance might draw more strongly on the capacity to select relevant information and overcome earlier suppression.

Furthermore, factors affecting performance in older adults and patients with semantic aphasia were examined. Older adults and patients with semantic aphasia might both show reduced flexibility in semantic cognition, since conceptual knowledge is thought to be largely preserved in both of these groups, relative to younger adults and age-matched controls, yet semantic control processes may be weakened. It was hypothesised that both groups would be disproportionately impaired at retrieving weak associations, which are thought to place higher demands on controlled retrieval (e.g., Badre et al., 2005). The thesis also investigates whether there would be any increase in within-category decline in categorisation in these groups. Within-category decline might reflect difficulty maintaining efficient categorisation in the face of building competition or retrieval-induced inhibition; consequently, it might be impaired in patients with semantic aphasia who have deficits of semantic control, and potentially also in older adults who might also have less controlled semantic retrieval. However, an alternative hypothesis is also possible: these groups might show *reduced* within-category decline, relative to younger adults, if this effect does not simply follow from the build-up of competition following earlier retrieval, but reflects a more active process of resolving competition through the suppression of associated memories. In other words, patients with SA and to some extent older adults may not deal with

the demands of initial retrieval by suppressing competitors, and this may make them less vulnerable to within-category decline.

Theme 3: Post-stroke fatigue and aphasia

Most patients with post-stroke aphasia experience cognitive fatigue – i.e., a sense of exhaustion after effortful language, cognitive and/or social processing – and this can be debilitating even for stroke survivors who have otherwise made a full recovery (Staub & Bogousslavsky, 2001). The relationship between fatigue and language impairment has rarely been examined, yet increasing difficulties in language and semantic retrieval could be related to this difficulty, since everyday situations such as having a conversation or understanding the environment are more challenging and may be more effortful. Most studies have used multidimensional self-reported questionnaires to measure post-stroke fatigue (Lynch et al., 2007), however, it is also not clear if patients always have insight into the effects that fatigue might have on their cognitive performance. These issues were explored using the PSST paradigm, along with a fatigue visual analogue scale (F-VAS; “0” – ‘not at all tired’ to “10” – ‘extremely fatigued’) to examine patients’ subjective feelings of fatigue. Effects of within-category decline and across-category decline in performance on the PSST were correlated with measures of semantic and executive impairment and with these subjective ratings of fatigue. Lastly, this research examined whether ‘refractory’ deficits in the classic word-picture matching task typically used in patients with aphasia would correlate with PSST performance and ratings of fatigue.

Theme 4: Role of LIFG in semantic control

Previous studies have shown important contributions of LIFG in resolving competition and in retrieving relevant aspects of semantic meaning (Badre et al., 2005; Bedny et al., 2008; Gold, Balota, Kirchoff, & Buckner, 2005; Pisoni et al., 2015; Schnur et al., 2009; Snyder, Banich, & Munakata, 2011; Thompson-Schill et al., 1997; Wagner et al., 2001). Studies of patients with semantic aphasia support this conclusion, as they typically have damage to LIFG and deficits of semantic control, although these lesions are not highly specific and often also affect additional regions in inferior parietal and/or posterior temporal cortex (e.g., Noonan et al., 2010). The research described above examining the PSST in patients with semantic aphasia therefore helps to characterise the role of LIFG in more controlled aspects of semantic retrieval. This work will determine whether lesions to left ventral prefrontal cortex have a negative influence on the initial accessibility of conceptual information (particularly weak associations), and whether these lesions change how retrieval changes over successive targets. In particular, if LIFG damage prevents the

resolution of competition or impairs controlled aspects of retrieval, patients with semantic aphasia might be expected to show greater impairment towards the end of each category. Conversely, if controlled retrieval by LIFG elicits retrieval-induced forgetting effects, these declines in comprehension might actually be reduced in patients relative to controls

There is also growing literature on the effects of non-invasive brain stimulation on lexical-semantic retrieval and selection, using transcranial direct current stimulation (tDCS), which modulates spontaneous brain activity within a region (Joyal & Fecteau, 2016). Stimulation of the left prefrontal cortex has been shown to decrease semantic interference effects within a semantic blocking naming paradigm (Pisoni et al., 2012; Wirth et al., 2011). This could possibly reflect strengthening of top-down control processes following LIFG stimulation, as anodal tDCS enhances cortical excitability and thus facilitates processes occurring within the stimulated brain areas. The PSST paradigm was used to examine the effects of anodal stimulation to LIFG, on multiple potentially interacting factors thought to influence semantic control demands. This study compared stimulation effects in the first half and second half of each category, since controlled retrieval demands may be initially high (in the absence of priming of semantically-relevant features). The strength of association between the probe category and the target was also manipulated, since controlled retrieval demands are higher for weakly-associated targets, and this effect should be particularly clear towards the beginning of each category in the absence of priming. Thus, it can be envisaged that tDCS could boost the retrieval of weak associations initially, but later have a more protective effect on the retrieval of strong associations by preventing decline during continuous categorisation. Lastly, the presence of distracting visual information during auditory semantic categorisation was also manipulated. Auditory targets were presented concurrently with relevant or irrelevant images to determine whether tDCS to LIFG would boost selective retrieval driven by the auditory input and ameliorate the effects of visual distractors. This design also permitted a comparison of the effects of LIFG stimulation on factors tapping selection/inhibition (presence of distracting visual information) and controlled retrieval (initial performance for weak vs. strong associations).

Thesis structure

Chapter 2 investigated if comprehension declines in healthy participants when semantically related items are presented at a rapid rate *without the repetition of individual items*. Across five experiments, several factors that might influence the magnitude of this effect were manipulated (speed of presentation; semantic relatedness; nature of semantic judgement; modality of presentation; presence of a secondary task). Experiment 1 investigated the effects of

speed of presentation and semantic relatedness (both factors that produce declining comprehension in patients with semantic access deficits) using thematic categories (e.g., PICNIC). Experiments 2 and 3 used taxonomic categories (e.g., VEHICLES) and specific feature judgements (e.g., colour RED) respectively, to establish whether within-category declines in comprehension were influenced by whether the items in the category shared most of their features (as in taxonomic categories) or only the goal-relevant feature (as in the specific feature-matching task). Experiment 4 examined semantic performance with ongoing categorisation using a two alternative-forced-choice paradigm, and investigated effects beyond verbal comprehension, by involving presentations of interleaved word and picture stimuli. Finally, within-category performance in categorisation was examined by the requirement to divide attention in a dual task study (Experiment 5). Therefore this chapter addresses Aims 1 and 2 above: the effects of stimuli and task on retrieval-induced declines in comprehension and how these factors may interact with the capacity for executive control.

Chapter 3 examined performance in older adults and SA patients, in terms of (1) the effect of strength of association (strong vs. weakly-related targets); (2) within-category decline – e.g., increasing problems categorising inputs when related targets have already been retrieved; (3) across-category decline – e.g., general cognitive fatigue which might produce deteriorating performance on the paradigm over the course of each testing session. Findings from this chapter are examined in three sections – (i) age comparisons, i.e., comparing performance of older adults with the younger adults from Experiment 1, Chapter 2; (ii) performance of SA patients in comparison with the older adults, and (iii) individual analysis of patients, examining relationships between performance on the PSST paradigm, subjective ratings of fatigue, performance on background semantic and executive tasks, and the magnitude of refractory effects in cyclical word-picture matching. This chapter therefore addressed Aims 2 and 3 above: the effect of reduced semantic control in the context of ageing and semantic aphasia on the magnitude of within-category decline, plus the relationship between these effects and post-stroke fatigue more generally.

Chapter 4 investigated if anodal tDCS to LIFG would modulate performance on the PSST paradigm in healthy young participants. The effects of stimulation on within-category decline and how this interacted with strength of association and the presence of irrelevant information (congruency of irrelevant visual images to auditory stimuli) were explored. Since LIFG is thought to support several aspects of semantic control, anodal stimulation to this region was expected to particularly benefit weak associations (which are thought to tap controlled semantic retrieval) and

categorisation in the presence of incongruent information (which might rely on semantic selection processes). Therefore this chapter is relevant to Aims 2 and 4: it helps to delineate the contribution of semantic control processes to retrieval-induced declines in comprehension, and the neural basis of this effect.

Chapter 5 discusses the findings of the thesis and draws general conclusions.

Chapter 2

When comprehension elicits incomprehension: Deterioration of semantic categorisation
in the absence of stimulus habituation

Acknowledgements: Stimuli for all experiments in this chapter were created and recorded with the help of Hannah Thompson. Experiment 4 was conducted in collaboration with an MRes dissertation student, Emma Davies, who helped with collecting images, and with data collection and analysis. Data collection in Experiment 5 was undertaken by Dominic Arnold.

Abstract

Since the pioneering work of Ebbinghaus, it has been known that repetition improves retrieval from memory; however, under some circumstances, it can also produce declining performance. Separate literatures have investigated this phenomenon, including studies showing poorer performance on naming and categorisation tasks when semantically-related items are repeated, subjective loss of meaning following “semantic satiation” and investigations of semantic “access deficits” in aphasia. Such effects have been explained in terms of interference from strongly activated competitors, longer-term weight changes, or habituation. There is also debate about the contribution of executive control mechanisms beyond the language/semantic domain. Moreover, many studies demonstrating declining performance used massed presentation of individual items, yet declining comprehension should occur for non-repeated items if the effects arise at the conceptual level: this pattern has been demonstrated for picture naming, but effects for categorisation are less clear. A paced serial semantic task was developed, in which healthy participants attempted to identify category members amongst distracters. Performance deteriorated with on-going retrieval for non-repeated words belonging to functional categories (e.g., PICNIC), taxonomic categories (e.g., ANIMAL) and goal-driven categories (e.g., colour RED – “tomato”, “post box”). In each case there was a release from semantic decline following a switch to a new category, demonstrating that this was not a general effect of time on task. The decline was observed across modalities when word and picture stimuli were interleaved, pointing to a conceptual locus, and it was greater for target words that were strong exemplars of a category. The effect was eliminated when decisions could be made at a slower presentation rate, and increased by conditions of divided attention, suggesting that categorisation may be achieved over time and supported by executive mechanisms. Therefore this work identified circumstances in which comprehension declines with on-going retrieval *without* stimulus repetition.

Introduction

Repetition and priming largely have beneficial effects: they facilitate processing efficiency (Wagner, Desmond, Demb, Glover, & Gabrieli, 1997) and increase the accessibility of memory representations (Radeau, Besson, Fonteneau, & Castro, 1998). A similar benefit of repetition occurs for semantically-related items, where DOG primes a related word such as CAT: such effects are often explained in terms of automatic spreading activation between associated concepts (Badre & Wagner, 2002; Neely, 1977a). Nevertheless, several largely separate literatures have reported *declining* comprehension and semantic access following massed repetition of semantically-related sets: (i) patients with semantic “access” deficits show declining comprehension when small sets of semantically-related items are presented repeatedly; (ii) items are reported to ‘lose their meaning’ in massed repetition studies in healthy participants; a phenomenon referred to as ‘semantic satiation’; (iii) psycholinguistic studies of healthy volunteers show poorer performance when semantically-related items are repeated: these effects are largely seen in picture naming, but can also affect comprehension (Campanella & Shallice, 2011; Harvey & Schnur, 2016; Wei & Schnur, 2015). In all of these separate literatures, there is a long-running debate about whether the effects arise at the lexical level (Crutch & Warrington, 2003; Damian, Vigliocco, & Levelt, 2001), within lexical-semantic links, or at the conceptual level (Belke, 2013; Gardner et al., 2012; Wei & Schnur, 2015). The underlying mechanisms are also unclear, with (a) some accounts proposing competition between currently-activated representations (Belke, Meyer, & Damian, 2005; Oppenheim, Dell, & Schwartz, 2010; Schnur, Schwartz, Brecher, & Hodgson, 2006), (b) other researchers noting that the effects are long-lasting, and are therefore more likely to reflect weight changes between associated items (Howard, Nickels, Coltheart, & Cole-Virtue, 2006; Oppenheim et al., 2010), or habituation of conceptual or lexical representations; and (c) patient studies emphasising that these effects are amplified by damage to executive processes outside the language/conceptual domain (Jefferies, Baker, Doran, & Ralph, 2007; Schnur et al., 2006). Finally, while many of these studies have involved the repeated presentation of individual items, declining comprehension should occur for non-repeated items if the effects arise at the conceptual level: research has already comprehensively demonstrated this pattern for picture naming (Belke, 2013; Harvey & Schnur, 2016; Howard et al., 2006) and this study examines parallel effects in comprehension (see also Wei & Schnur, 2015).

Patients with semantic access impairment show “refractory effects”, or declining comprehension in cyclical word-picture matching tasks (Jefferies et al., 2007; Warrington & McCarthy, 1983). When sets of semantically-related items are repeatedly presented, such that the

target on one trial becomes a distractor on the next, patients become increasingly unable to select the target (Humphreys, 1997; Warrington & Cipolotti, 1996; Warrington & Crutch, 2004). This phenomena is only observed when the interval between one stimulus and the next is short (Campanella, Mondani, Skrap, & Shallice, 2009; Jefferies et al., 2007) and when the items are highly related in meaning (Cipolotti & Warrington, 1996; Crutch & Warrington, 2008; Forde & Humphreys, 1995; Forde & Humphreys, 1997; Jefferies et al., 2007). These effects have largely been documented in verbal comprehension tasks – i.e., word-picture matching (Cipolotti & Warrington, 1996; Jefferies et al., 2007; Schnur et al., 2006; Warrington & McCarthy, 1983; Warrington & Crutch, 2004). However, they have also been demonstrated in non-verbal judgements such as picture-picture matching (Forde & Humphreys, 2007; Gardner et al., 2012; Thompson, Robson, Lambon Ralph, & Jefferies, 2015), suggesting semantic access deficits can occur at an amodal conceptual level. The mechanism that underpins this effect is somewhat unclear (Mirman, 2011): it has been linked to a difficulty overcoming post-retrieval inhibition (Gotts & Plaut, 2002) or to strong competition when several potential responses are activated (Forde & Humphreys, 1997; Jefferies et al., 2007; Schnur et al., 2006). The effect is strongest in patients with damage to prefrontal cortex (Campanella et al., 2009; Gardner et al., 2012; Schnur et al., 2006; Thompson et al., 2015), suggesting that it may reflect damage to control mechanisms that are necessary to maintain performance in the presence of strong competition (i.e., on later trials when all potential responses are strongly primed) and/or to overcome post-retrieval inhibition (i.e., when targets have to be re-selected having being inhibited on previous trials). In line with this view, patients with semantic aphasia (SA) show deficient semantic control across verbal and non-verbal tasks, characterised by difficulty supressing irrelevant aspects of knowledge and comprehending distant relationships and ambiguous meanings (Corbett, Jefferies, & Ralph, 2011; Jefferies & Lambon Ralph, 2006; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010). These deficits give rise to declining comprehension in both cyclical word-picture matching and picture-picture matching (Gardner et al., 2012; Thompson et al., 2015).

Healthy participants typically do not show declining performance on cyclical word-picture or picture-picture matching tasks (Damian et al., 2001; Riley, McMahon, & de Zubicaray, 2015; some exceptions discussed below), although they do show increasing latencies in cyclical picture naming studies when sets of semantically-related items are named repeatedly (Kroll & Stewart, 1994; Vitkovitch & Humphreys, 1991). In some previous studies, these effects were explained in terms of competition from activated conceptual representations at the point of lexical selection: items drawn from the same semantic category activate each other within the conceptual system via their shared features, and this might hinder retrieval of a specific object name because other

activated concepts act as competitors (Belke, 2008; Belke et al., 2005; Damian et al., 2001). “Semantic blocking” effects in naming are sensitive to semantic variables, such as the strength of the association between the items (Abdel Rahman & Melinger, 2011), supporting the view that they reflect processes at the conceptual level.

A continuous picture naming paradigm can also elicit declining performance when conceptually-related items are presented (i.e., two animals) without the repetition of individual items (Belke & Stielow, 2013; Belke, 2013; Howard et al., 2006; Kleinman, 2013; Navarrete, Mahon, & Caramazza, 2010; Oppenheim et al., 2010; Runnqvist, Strijkers, Alario, & Costa, 2012; Schnur, 2014). For example, in the sequence GOAT, CAR, TOMATO, TRUCK, HORSE, the naming time for HORSE would be slower than that for GOAT due to their conceptual overlap, and this effect is found even at long ‘lags’ with many unrelated intervening items. Since this effect appears to be relatively long-term (cf. Wheeldon & Monsell, 1994), it may reflect cumulative weight changes: each time an item from the animal category is named, the associative links to other animal exemplars might be strengthened and this could increase competition on future trials (Howard et al., 2006). Oppenheim et al. (2010) proposed that this type of incremental learning might not only reinforce the connections between semantic and lexical representations of targets, but also weaken the semantic-lexical links for non-targets. Thus, semantic interference effects in naming can arise as a direct consequence of retrieval that renders related items less accessible (see also Anderson, Bjork, Bjork, & Jordan, 2000, for a related phenomenon in memory).

Several recent studies used a continuous paradigm without item repetition to examine categorisation as opposed to picture naming, and observed cumulative *facilitation* as opposed to inhibition (Belke, 2013; Riley et al., 2015). Nevertheless, under some circumstances, healthy controls can show *declining* categorisation with repetition (Harvey & Schnur, 2015), and thus resemble patients with semantic access impairment. This pattern was observed in cyclical matching to a deadline when there were repeated presentations of the same target plus minimal delays between trials (Campanella & Shallice, 2011): these circumstances potentially create competition between the current target and previous targets (which have become distractors), with little time to resolve this competition or to recover from previous processing. In addition, Wei and Schnur (2015) reported semantic interference in a picture matching task, when the same response options were repeatedly used to probe associations with either related or unrelated concepts; in this study, there was initial facilitation (when semantically-related items were repeated at short lags; perhaps reflecting faster visual recognition for the probe when immediately following a related item), followed by longer-lasting inhibition (when related trials

occurred at longer lags, perhaps reflecting response interference when a similar probe had led to a different decision on a previous trial).

Long-lasting declines in comprehension with repetition have also been reported in a third set of studies on “semantic satiation”: this research reports that prolonged inspection and repetition of words results in a subjective loss of meaning (Jakobovits & Lambert, 1962; Smith & Klein, 1990). Semantic judgements are slowed under these circumstances but there is little effect on tasks such as lexical decision, suggesting that this effect again reflects effects at a semantic level (Cohene, Smith, & Klein, 1978; Neely, 1977b; Smith, 1984). Repetition is thought to cause temporary blocking of access to conceptual information (Frenck-Mestre, Besson, & Pynte, 1997; Pynte, 1991), potentially reflecting effects akin to neural fatigue or adaptation (Jakobovits & Lambert, 1962; Lambert & Jakobovits, 1960; Smith & Klein, 1990). Explanations for semantic satiation effects are similar to those above in that they anticipate spreading activation to related conceptual representations; these conceptual representations then become “habituated” via repeated exposure, disrupting category judgements. The proposal of long-lasting semantic interference and semantic satiation could therefore be related, and similar to the effects of repeatedly retrieving one aspect of knowledge, which suppresses related concepts, even when these concepts are probed in a novel way (Anderson et al., 2000). However, it is unclear what determines whether semantic similarity will produce facilitation or inhibition in subsequent conceptual retrieval, and when these effects emerge.

The current study used a paced serial semantic task (PSST), in which healthy participants monitored a stream of inputs and pressed a button every time they detected a target that matched a particular category. Neither targets nor distracters were repeated – therefore, the task resembled a continuous naming paradigm but required the comprehension and categorisation of meaningful inputs, rather than the production of speech. Demonstrations of declining semantic performance thus far have utilised repeated presentations of the same items (either as targets or as distracters; Campanella & Shallice, 2011; Harvey & Schnur, 2015; Wei & Schnur, 2015) – it is unclear if the same effects would emerge in the absence of item repetition (especially since research using the continuous paradigm has found *facilitation* in the absence of item repetition; Belke, 2013; Riley et al., 2015). This study considers the ability of participants to sustain semantic processing over time: both *within* categories – by examining whether comprehension deteriorated over the course of each category as more related targets were presented, and *between* categories – by quantifying changes in performance across the experiment, as participants became generally fatigued. Changes in the accessibility of meanings with on-going

categorisation, in the absence of massed repetition, would have important implications for every-day comprehension.

Performance on this task might deteriorate with the on-going classification of related targets if: (i) there is spreading activation to related concepts that share semantic features, and (ii) if this spreading activation creates competition at the point of classifying a new target, or causes longer-term weight changes (i.e., suppression of related concepts as successive items are classified; cf. Oppenheim et al., 2010). Competition or longer-term suppression of items that become targets is likely to increase the requirement for semantic control – either through selection/inhibition mechanisms that can resolve competition, or through the promotion of weak (i.e., previously suppressed) but currently-relevant information in a process of “controlled retrieval” (cf. Badre, Poldrack, Paré-Blagoev, Inslar, & Wagner, 2005). Under these circumstances, we might expect participants to have greater difficulties in retrieving items presented later in the category when executive resources are limited, since this would interfere with selection and/or controlled retrieval. Thus, the PSST paradigm allowed for the manipulation of factors linked to both semantic representations themselves – such as strength of association, which should influence the spread of activation to related concepts – and factors linked to control processes that are thought to play critical role in focussing retrieval on currently-relevant knowledge in the face of strong distractors or weak targets – such as conditions of divided vs. undivided attention. In this way, the task maps onto contemporary accounts of semantic processing, which envisage amodal concepts that interact with control processes to support context- and task-appropriate semantic retrieval (Lambon Ralph, Jefferies, Patterson, & Rogers, 2016).

In five experiments, factors that might influence the extent to which comprehension declines with continuous semantic decisions were manipulated. In Experiment 1, the speed of presentation and semantic relatedness were investigated (both factors that produce declining comprehension in patients with semantic access deficits). The declining performance observed for thematic categories was replicated using taxonomic and specific feature judgements (Experiments 2 and 3), and the same pattern of declining semantic performance was found with on-going categorisation using a two alternative-forced-choice paradigm (Experiment 4). It was also examined whether the effect extended beyond verbal comprehension to a task involving interleaved word and picture stimuli, to establish if this effect has a conceptual locus (which should transfer between modalities), as opposed to a lexical one (cf. Thompson et al., 2015; Wei & Schnur, 2015). Finally, this study investigated whether the within-category decline in categorisation was increased by the requirement to divide attention in a dual task study, as would

be expected if executive mechanisms guide selection in the face of strengthening competition from semantically-related items (Experiment 5). Taken together, these studies characterise how semantic cognition declines without item repetition as a consequence of sustained retrieval within a broadly-activated conceptual field, providing a mechanism by which meaning can change in a dynamic fashion during on-going cognition.

Experiment 1: Effect of speed of presentation and strength of association on a thematic categorisation task

Rationale

If the ability to maintain semantic retrieval declines over time (even in the absence of explicit item repetition), as a consequence of processing related items, this experiment would show: (i) decline in comprehension within a category but then release from this effect when the task switches to a new category and (ii) a stronger decline in comprehension when targets are strongly-related as opposed to weakly-related to the category, since strongly-related items will accrue activation from earlier trials to a greater extent than weakly-related targets. This could lead to greater competition on strongly-related trials (if residual activation of previously-presented related items interferes with current semantic decisions; Belke et al., 2005; Schnur et al., 2006), or increased retrieval difficulty for related targets, following adaptation of conceptual information or cumulative weight changes that strengthen previous targets and weaken previous non-targets (Howard et al., 2006; Oppenheim et al., 2010). Similarly, patients with semantic access deficits show declining cyclical word-picture matching for sets of closely related items – but not for sets of repeated but unrelated or distantly-related items (Crutch & Warrington, 2003). Warrington and Cipolotti (1996) found a detrimental effect of cycle in these patients even when items in the last cycle were replaced with new items from the same category, suggesting that spreading activation between strongly-related concepts is the likely cause of this decline. The literature on semantic satiation also shows stronger detrimental effects of repetition for strong vs. weak associates (Balota & Black, 1997). Therefore decline in performance was compared for strong and weak members of a thematic category (e.g., PICNIC – strong category member = “sandwich”, weak category member = “wasp”).

Previous research has also found declining performance in cyclical word-picture matching paradigms with fast but not slow presentation speeds, perhaps because rapid presentation allows a build-up of competition from previously-presented semantically-related items, and this takes time to resolve (Campanella & Shallice, 2011). Cyclical paradigms may be sensitive to increasing

levels of competition, since they involve selecting a target from amongst close distractors, suppressing this item as it becomes a distractor on the next trial, and then re-selecting it on the subsequent cycle. Campanella and Shallice (2011) found that when a deadline was imposed in these circumstances, performance deteriorated as cycles of related items were repeated. In contrast, performance in continuous paradigms declines following retrieval of related information over the long-term term, and satiation effects occur when inputs are presented for long durations (Smith, 1984). Declining performance in these circumstances may be less related to competition from on-going activation and more to do with cumulative weight changes (Oppenheim et al., 2010) and/or adaptation, which may be less sensitive to speed of presentation. Therefore performance was contrasted at a relatively fast speed of presentation (1.1s) with a slower speed (2s) to establish whether this manipulation would alter the extent to which semantic categorisation declined in the PSST paradigm. The task resembled a vigilance task, in that it required sustained attention to a category over time and button pushes to targets but not to distractors. This method allowed rapid presentation of successive items and therefore it was hypothesised that it could create ideal circumstances for cumulative decline in continuous categorisation.

Method

Participants: 24 undergraduate students (16 females and 8 males) from the University of York participated in the experiment in exchange for course credit or a payment of £5. The mean age of the students was 19 years (range of 18-24). All participants were native English speakers. Ethical approval was obtained from the Department of Psychology Ethics Committee at the University of York. All participants gave written informed consent.

Task and Design: The 'Paced Serial Semantic Task' or PSST required rapid semantic association judgements that linked spoken words to a thematic category, such as PICNIC or HOSPITAL. Participants were asked to classify spoken words in terms of whether they were associated with the target categories. Two factors were manipulated in a repeated-measures design: (1) the strength of association between the target and category (strong or weak), and (2) presentation speed (fast: 1.1s or slow: 2s). The experiment additionally looked at (3) effects of 'within-category fatigue' (comparison of task performance in the first half compared with the second half of each category), and (4) 'across-category fatigue' or decline in performance across the testing session.

Materials: Twenty different category labels were used (such as PICNIC) with 60 items in each category. 20 items were related to the category, including 10 targets that were strongly related to the category label, such as “sandwich”; and 10 that were distantly related, such as “wasp”, while the remaining 40 items were unrelated to the category (e.g. “exam”) – these were recycled items from other categories (see Appendix C for a complete list of items used). Target words were selected using the Edinburgh Associative Thesaurus (EAT; Kiss, Armstrong, & Milroy, 1973), supplemented by a pilot study in which ratings were collected for the relatedness of each word to the category label. Participants (N = 16) used a 7-point Likert scale to judge relatedness, and items were categorised as strongly related (> 5.5), weakly related (2.2 - 5.5) or unrelated (< 2.2).

Procedure: The experiment was presented using E-Prime 2.0 (Psychology Software Tools, Sharpsburg, PA). Category names were presented as written words that remained visible throughout the block, to reduce demands on working memory. There was an equal distribution of strong and weak targets in the first and second half of each category. The order of categories and items was fully counterbalanced between subjects (there were parallel versions of the experiment utilising two presentation orders; each of these was presented to half of the participants, such that effects at the group level could not reflect effects specific to one order of presentation). These details were repeated across all experiments below.

Participants were asked to press ‘1’ each time they heard a word that was related to the category, and not to press for unrelated words. Thus the task required sustained and rapid attention to semantic information. Each participant was presented with all 20 categories, 10 at one speed (e.g., with a 1.1 second gap between each auditory word) and 10 at another speed (e.g., 2 second ISI), with the two speeds counterbalanced using an ABBA or BAAB design.

Results

The main dependent measure in all experiments was response sensitivity (d'), which accounts for response bias (the general tendency to respond *yes* or *no*; Stanislaw & Todorov, 1999). A higher d' score reflects better response sensitivity (i.e., the ability to correctly recognise targets and reject distractors – as opposed to making ‘false alarms’ on non-target items). As there was an equal distribution of strong and weak targets in the first half and second half of each category, within-category changes in performance were examined by computing d' separately for these two halves of each category. In Experiment 1 and subsequent experiments generalised linear models (GLMs, using generalised estimating equations) were used to analyse response

sensitivity for each category and for each participant, including within-subject fixed-effects of within-category position (first vs. second half of each category), across-category fatigue (first vs. second half of the entire experiment), speed of presentation (1.1 vs. 2s), and semantic relatedness (d' scores computed separately for targets that were strongly or weakly related to the category), in a fully-factorial model that included all interaction terms for these predictor variables. These d' scores were therefore computed across sets of trials, retaining information about performance per category per participant (i.e., categories were treated in the same way as individual trials in a classic 'by-items' analysis). The GLMs allowed for random variation in the intercept across participants. Average RT was entered for each of the first and second half of each category as a covariate (i.e., the average RT for correct responses per condition and participant) in this and all subsequent GLMs. Given that the task required participants to respond before a deadline (i.e., before the onset of the next item, rather than as quickly as possible), RT was not expected to be sensitive to the effects of interest but by including average RT as a covariate in the analysis, changes in RT were accounted for over the course of a block of trials. This would allow focus on response sensitivity while simultaneously accounting for the possibility of a response accuracy trade-off.

Response sensitivity in each condition is shown in Figure 2.1. Table 2.1 shows the results of the GLM analysis (alongside conventional repeated-measures ANOVA of response sensitivity, which revealed the same effects of the experimental factors). There was a main effect of speed, indicating better performance at a slower rate of presentation. There was also a main effect of association strength: sensitivity was lower for weakly related items in comparison to stronger associations. There was no significant main effect of within-category position or across-category fatigue ($p > .1$). However, there was a significant interaction of relatedness and within-category decline: participants made more errors in categorisation towards the end of each category especially for the strongly associated targets. Post-hoc tests with Bonferroni correction indicated this decline in sensitivity 'within' each category affected performance on strongly related targets: $t(23) = 2.34, p = .028$, but not weakly related targets: $t(23) = .105, p = .917$. There was also a significant interaction between speed and relatedness: participants found it harder to identify weak items at the faster speed in comparison to the slower speed. Bonferroni corrected t-tests indicated significant effects of relatedness at both speeds, with a larger effect at the fast speed: $t(23) = 7.64, p < .001$, in comparison to the slow speed: $t(23) = 5.37, p < .001$. All other interaction terms were non-significant. A more detailed breakdown of performance, showing hits, correct rejections, false alarms and misses, is reported in Table 6.1 in Appendix A. This shows few false alarms, instead, participants tended to fail to respond to targets when performance was poor.

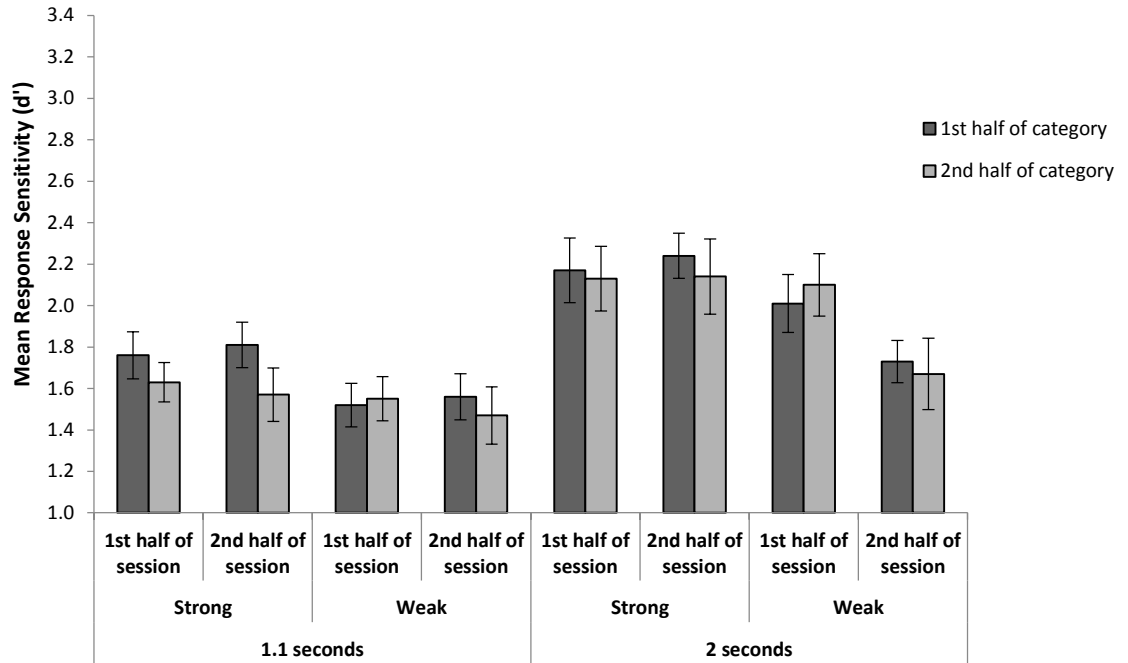


Figure 2.1: Mean response sensitivity (d') in Experiment 1 (Thematic-matching), for the first and second half of each category (within-category fatigue) and across the testing session (across-category fatigue), split by strong and weak targets, at the two presentation speeds. Error bars show SE of the mean.

Table 2.1: Summary of significant results for response sensitivity from GLM and repeated-measures ANOVA analysis, examining effects of speed and relatedness, plus within-category and across-category changes in performance, in Experiment 1: Thematic-matching.

Experiment 1: Thematic-matching			
		GLM (RT covariate)	ANOVA
Fixed effects:	df	Wald χ^2, p	F, p
Across-category	(1, 23)	$p > .1$	$p > .1$
Within-category	(1, 23)	$p > .1$	$p > .1$
Relatedness	(1, 23)	52.45, $p < .001$	50.26, $p < .001$
Speed	(1, 23)	40.25, $p < .001$	38.57, $p < .001$
Interactions:			
Within-category x Relatedness	(1, 23)	29.31, $p < .001$	28.09, $p < .001$
Speed x Relatedness	(1, 23)	17.62, $p < .001$	16.89, $p < .001$
Speed x Within-category	(1, 23)	$p > .1$	$p > .1$
Across-category x Relatedness	(1, 23)	3.24, $p = .072$	3.10, $p = .091$

Footnote: Table presents two parallel analyses employing (i) mixed effects modelling (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) analysis of variance. Other interaction terms were non-significant ($p > .1$).

Summary of Experiment 1

Even though individual words were not repeated, as in typical semantic satiation or cyclical matching experiments, performance showed a cumulative decline across the targets in each category. Within-category decreases in response sensitivity were greater for targets strongly associated with the category label (e.g., PICNIC – “sandwich”), compared with weakly associated targets (e.g., PICNIC – “wasp”). Performance on the task was also influenced by speed of presentation: participants showed poorer performance at faster speeds. Thus, the PSST revealed several of the hallmarks of “semantic refractory effects” in healthy subjects – namely, declining performance with on-going semantic retrieval; greater effects when there was little time to recover between trials (Warrington & McCarthy, 1983) or a deadline to respond (Campanella & Shallice, 2011); plus a more substantial decline for more strongly-related items, suggesting that this effect reflects the spread of activation within semantic representations. There was no decline in performance over the course of the experiment (i.e., across-category fatigue effects were not significant).

Experiment 2: Taxonomic category matching

Rationale

This experiment provided a replication of the within-category decline effect in Experiment 1 using taxonomic categories as opposed to thematic categories. The target items shared common features (e.g., eyes and fur, for the category ANIMALS). If within-category decline reflects spreading activation within the semantic system that interferes with the categorisation of incoming items, this effect should be observed for targets with strong featural overlap.

Method

Participants: 24 undergraduate students (16 females and 8 males) were recruited from the University of York, and received course credit or a payment of £5 for their participation. The mean age of the students was 21 years (range of 18-30). All participants were native English speakers. All participants gave written informed consent.

Task and procedure: Targets were strong members of each taxonomic category (e.g., “apple”, “orange”, “grapes” for FRUITS). Twenty different category labels were used (VEHICLES, FLOWERS, BIRDS, etc.). For each category, there were 20 related items (e.g., VEHICLES – “car”) and 40 unrelated items (e.g., VEHICLES – “meerkat”) in each category – the unrelated items were targets from other categories (see Appendix D for a complete list of items used). Unlike Experiment 1, this

experiment did not include manipulations of speed or relatedness. Items were presented at a speed of 1.1s. The experiment was presented using E-prime 2.0 (Psychology Software Tools, Sharpsburg, PA).

Results

Response sensitivity is shown in Figure 2.2. The effects of two fixed-effects were examined in a GLM: (1) 'across-category fatigue' (comparison of task performance in the first half of session compared with the second half of session); and (2) 'within-category decline' (comparison of task performance in the first compared with the second half of each category) in a fully factorial model, including RT as a covariate of no interest. A parallel analysis using repeated-measures ANOVA revealed the same pattern of results; see Table 2.2 for *Wald* χ^2 , *F* and *p* values.

The GLM analysis found a significant main effect of within-category decline, indicating poorer performance towards the end of each category. There was little evidence that performance changed across the experiment (i.e., no across-category effect). There was also no significant interaction of within-category and across-category decline.

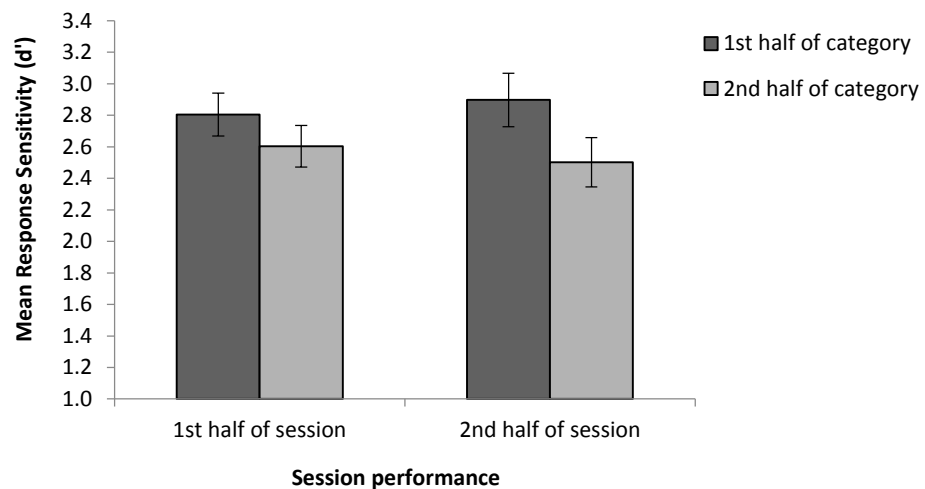


Figure 2.2: Mean response sensitivity (d') in Experiment 2 (Taxonomic-matching), for the first and second half of each category (within-category fatigue) and across the testing session (across-category fatigue). Error bars show *SE* of the mean.

Table 2.2: Summary of significant results for response sensitivity from GLM and repeated-measures ANOVA analysis, examining effects of within-category and across-category changes in performance, in Experiment 2: Taxonomic-matching.

Experiment 2: Taxonomic-matching			
		<i>GLM (RT covariate)</i>	<i>ANOVA</i>
Fixed effects:	<i>df</i>	<i>Wald χ^2, p</i>	<i>F, p</i>
Across-category	(1, 23)	<i>p > .1</i>	<i>p > .1</i>
Within-category	(1, 23)	<i>24.89, p < .001</i>	<i>23.85, p < .001</i>
Interactions:			
Across-category x Within-category	(1, 23)	<i>p > .1</i>	<i>p > .1</i>

Footnote: Table presents two parallel analyses employing (i) mixed effects modelling (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) analysis of variance.

Summary of Experiment 2

Taxonomic categorisation was easier overall than the thematic judgements used in Experiment 1 (as reflected in larger d' scores). However, a similar pattern of declining performance within each category was observed, which did not vary across the testing session, indicating that the results were not a consequence of a general difficulty in sustaining attention to the task.

Experiment 3: Specific feature matching

Rationale

Experiment 3 investigated whether the within-category semantic decline observed in Experiments 1 and 2 would occur when items were categorised on the basis of single feature, such as colour (e.g., “post-box”, “tomato” and “Santa” for the category RED). Feature matching is a demanding semantic task that requires executive resources to focus semantic retrieval on the feature relevant to the task, and away from dominant aspects of knowledge (Badre et al., 2005; Jefferies, 2013): targets in this experiment were not globally related to the category being probed, and shared few (if any) features, except for the feature specified in the instructions (e.g., the targets “pancakes”, “blackboard”, “postcard” share the feature FLAT but are not globally related). If the requirement to maintain a narrow focus of conceptual retrieval underpins the pattern of deteriorating categorisation, these effects would be expected to be maintained in this experiment. If, in contrast, strong global semantic relationships between target items are

necessary for within-category decline in performance, this effect should be reduced in magnitude or even eliminated in this experiment.

Method

Participants: There were 24 participants (18 females and 6 males); recruited from the University of York, in exchange for course credit or payment of £5. Mean age of the students was 19 years (range of 18-24). All participants were native English speakers. All participants gave written informed consent.

Task and procedure: The paradigm was similar to that in Experiment 2, except categorisation was based on a specific feature of the presented items. For example, participants were shown a category, such as RED and were asked to classify spoken words (such as, “tomato”, “post-box”, “Santa”), in terms of whether they matched this specific feature. Twenty-two different category labels were used (e.g., NOISY, FLAT, HOT, etc.) with 60 items in each category: 20 were related items (e.g., NOISY – “vacuum cleaner”), and 40 were unrelated items (e.g., NOISY – “caramel”) taken from other categories (see Appendix E for a complete list of items used). Each participant was presented with all 22 categories. The order of categories and items was fully counterbalanced between subjects.

Results

Results are shown in Figure 2.3. This experiment assessed the effects of two within-subjects factors in a GLM: (1) ‘across-category decline’ (comparison of task performance in the first half of the experiment compared with the second half); and (2) ‘within-category decline’ (comparison of task performance in the first compared with the second half of each category). These fixed effects were entered into a fully-factorial model. A parallel analysis using repeated-measures ANOVA was conducted on sensitivity, which yielded similar results (see Table 2.3 for *Wald* χ^2 , *F* and *p* values).

There was a significant main effect of within-category decline: performance was better at the beginning than the end of each category. There was no main effect of across-category decline ($p > .1$). There was a significant across-category by within-category interaction, indicating a greater decline in performance ‘within’ each category towards the end of the experiment (see Figure 2.3). This was supported by Bonferroni t-tests, which indicated a highly significant within-category decline for the second half of the session: $t(23) = 4.40$, $p < .001$, but not for the first half of the session ($p > .1$).

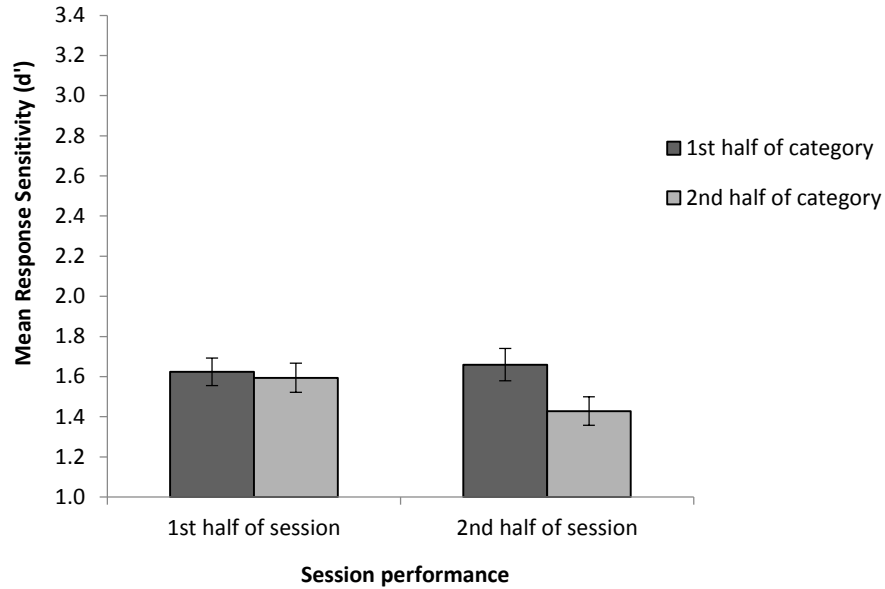


Figure 2.3: Mean response sensitivity (d') in Experiment 3 (Feature-matching), for the first and second half of each category (within-category fatigue) and across the testing session (across-category fatigue). Error bars show SE of the mean.

Table 2.3: Summary of significant results for response sensitivity from GLM and repeated-measures ANOVA analysis, examining effects of within-category and across-category changes in performance, in Experiment 3: Feature-matching.

	Experiment 3: Specific feature-matching		
		GLM (RT covariate)	ANOVA
Fixed effects:	df	Wald χ^2, p	F, p
Across-category	(1, 23)	$p > .1$	$p > .1$
Within-category	(1, 23)	13.43, $p < .001$	12.87, $p = .001$
Interactions:			
Across-category x Within-category	(1, 23)	6.18, $p = .013$	5.93, $p = .025$

Footnote: Table presents two parallel analyses employing (i) mixed effects modelling (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) analysis of variance.

Summary of Experiment 3

This experiment provided a second replication of the cumulative decline in categorisation performance within categories, in the absence of item repetition; however, in this case, the pattern was only apparent in the second half of the session. The feature-based classification task used in Experiment 3 was more demanding than the thematic and taxonomic categorisation tasks used in Experiments 1 and 2, and the within-category decrease in performance on this

executively-demanding semantic task might have been maximal towards the end of testing session, when cognitive control was likely to be lower. Most importantly, this experiment shows that the within-category decline effect extends to situations in which there is not a strong global relationship between the targets. The effect might therefore not emerge from strengthening activation in sets of globally-related concepts, but might instead reflect interactions between semantic goal representations (i.e., targets are 'thin', or 'red', or 'round') and the conceptual store.

Experiment 4: Within-category decline in categorisation across modalities

Rationale

Experiment 4 considers whether the systematic decline in the meaning of an item occurs in a manner that is independent of a specific modality. Declining performance in the cyclical matching paradigm in patients with aphasia has largely been documented using verbal comprehension tasks – i.e., word-picture matching (Cipolotti & Warrington, 1996; Jefferies et al., 2007; Schnur et al., 2006; Warrington & McCarthy, 1983). It has been suggested that this effect may be exclusive to auditory or verbal materials (Crutch & Warrington, 2008; Warrington & Crutch, 2004). Similarly, in healthy participants, declining performance on cyclical paradigms has been linked to lexical competition during speech production (rather than conceptual retrieval) (e.g., Belke et al., 2005; Harvey & Schnur, 2015; Howard et al., 2006), while in the satiation literature, it has been suggested that declining comprehension comes about due to adaptation of orthographic-to-semantic links (Tian & Huber, 2010) – consequently, these effects of repetition may be restricted to the verbal domain. Nevertheless, SA patients show declining performance across cycles for both word-picture and picture-picture matching tasks (Forde & Humphreys, 2007; Gardner et al., 2012), suggesting that semantic access deficits can occur at an amodal conceptual level, and similar results were obtained recently in healthy participants (Wei & Schnur, 2015). This is consistent with the proposal that semantic cognition draws on amodal representations and control processes that operate across modalities. This study characterised the decline in performance for word targets, picture targets and an interleaved condition in which related items were presented as both words and pictures on different trials. If the decline in performance arises at a conceptual level, this effect should not be diminished for the interleaved condition. This pattern would allow ruling out accounts of within-category decline that involve fatigue/adaptation or competition within lexical-level representations.

In this experiment, the PSST paradigm was also modified: participants were asked to make a response on each trial (pressing one of two buttons to indicate if the item was a member of the category, or not), and there were equal numbers of targets and distractors. This two alternative-forced-choice (2AFC) design allowed minimising the effects of response bias (relative to the paradigm used above, in which participants only responded when a target was present) and, most importantly, to characterise within-category changes in performance not only in terms of hits but also correct rejections, to examine if participants were updating their working definition of the category over the set of trials. If participants showed a similar within-category reduction in accuracy for both targets and non-targets, it would suggest reduced ability to retrieve the relevant information, while if they only showed a change for targets; it could suggest a narrower definition of the category is being acquired as the category progresses (i.e., a shift in response criteria).

Method

Participants: 24 participants, native English speakers aged between 18-30 years old, were recruited from the University of York in exchange for course credit or a payment of £5. All participants gave written informed consent.

Task and Design: The target categories in this experiment were thematic, in line with Experiment 1. Within-category manipulations involved: (i) stimulus modality (auditory words, pictures and interleaved auditory words and pictures) and (ii) within-category position (first half of each category was compared to the second half). The effect of across-category fatigue was not examined in this experiment, since performance would have been influenced by the order in which the three modality conditions were presented. Strength of association ratings were also used to split the verbal targets into strong and weak. The effect of this factor is reported in a cross-experiment comparison below.

Materials: There were 30 categories, 10 per modality (words, images, interleaved). Each participant saw each category only once (in one of the three modality conditions). There were 40 items in each category (20 related and 20 unrelated to the category). In the visual condition, the images were colour photographs on a white background. In the auditory condition, the word stimuli were audio files (see Appendix F for a complete list of items used).

Procedure: The experiment was presented using E-Prime 2.0 (Psychology Software Tools, Sharpsburg, PA). Participants completed 15 practice trials (5 trials for each modality), before proceeding to the experimental trials. At the start of each category block, the category label was

written on screen until the participant pressed the spacebar to continue. Pilot testing indicated that participants were unable to perform the interleaved condition at 1.1s, so a slightly slower presentation speed of 1.3s was adopted. Each item was presented for 1.3s and this was the deadline for responding. Participants pressed one of two buttons to indicate if the item was related or unrelated to the target category. The order of stimulus modality, categories, and items within each category was fully counterbalanced across participants (although in the interleaved condition, a spoken word was followed by a picture).

Results

Results are shown in Figure 2.4. The GLM included *modality* (words vs. pictures); *interleaving* (single modality vs. interleaved words/pictures), and *within-category decline*, as fixed within-subjects effects and controlled for RT as a covariate. Parallel analysis using repeated-measures ANOVA on response sensitivity obtained similar results (see Table 2.4 for *Wald* χ^2 , *F* and *p* values).

There was a main effect of interleaving: lower performance for interleaved vs. non-interleaved trials. There were no other main effects ($p > .1$). There was an interaction between within-category decline and interleaving: the cumulative decrease in performance 'within' each category was larger for interleaved than non-interleaved trials. This was supported by post-hoc tests, which indicated a significant decline for the interleaved condition: $t(21) = 2.17, p = .042$, but not the non-interleaved trials ($p > .1$). There was also a significant interaction between modality and interleaving conditions, reflecting a greater effect of interleaving for pictures than words. Bonferroni corrected t-tests indicated a highly significant effect of interleaving in the pictures modality: $t(21) = 3.20, p = .004$, but not the words modality ($p > .1$). Other interactions were not significant ($p > .1$).

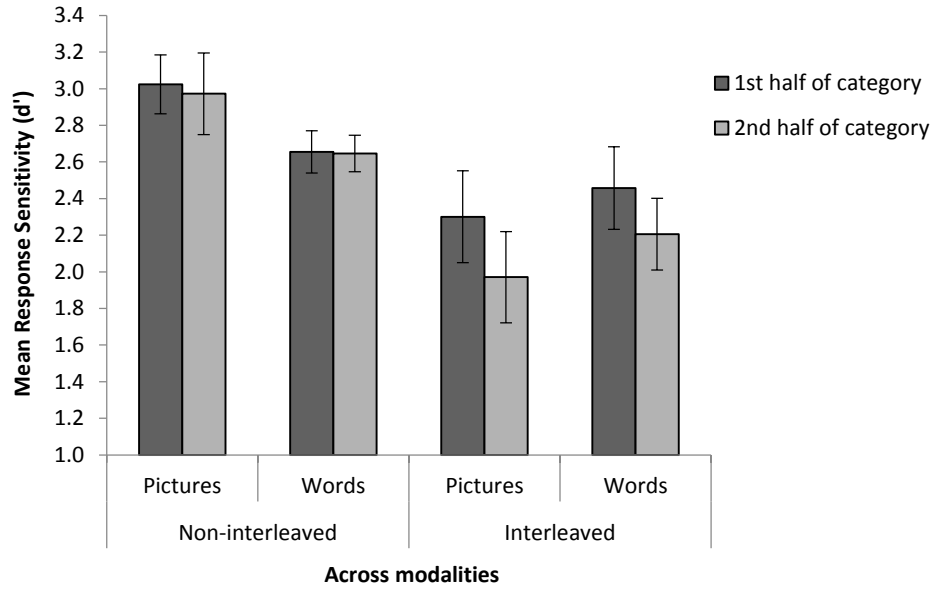


Figure 2.4: Mean response sensitivity (d') in Experiment 4 (Effect across modalities), shown individually for the pictures and words modality in the interleaved and non-interleaved conditions, in the first and second half of each category (within-category decline), Error bars show SE of the mean.

Table 2.4: Summary of significant results for response sensitivity from GLM and repeated-measures ANOVA analysis, examining effects of modality and interleaving, plus within-category changes in performance, in Experiment 4: Cross-modality alternative-forced-choice decisions.

Experiment 4: Across modalities			
		GLM (RT covariate)	ANOVA
Fixed effects:	df	Wald χ^2, p	F, p
Within-category	(1, 21)	$p > .1$	$p > .1$
Modality	(1, 21)	$p > .1$	$p > .1$
Interleaved	(1, 21)	15.72, $p < .001$	15.03, $p = .001$
Interactions:			
Modality x Interleaved	(1, 21)	7.39, $p = .007$	6.59, $p = .018$
Interleaved x Within-category	(1, 21)	4.85, $p = .028$	4.48, $p = .046$
Modality x Within-category	(1, 21)	$p > .1$	$p > .1$
Modality x Interleaved x Within-category	(1, 21)	$p > .1$	$p > .1$

Footnote: Table presents two parallel analyses employing (i) mixed effects modelling (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) analysis of variance.

Summary of Experiment 4

In an alternative design using 2AFC decisions a within-category decline was observed for both words and pictures, demonstrating that this effect does not reflect habituation or competition within lexical-semantic representations. Thus, within-category decreases in categorisation appear to reflect processes at an amodal conceptual level. The within-category decline effect was also more marked for interleaved blocks, containing both word and picture targets, relative to single-modality blocks, suggesting that the effect can accumulate across these inputs. Interleaved blocks were more difficult, presumably because of the greater need for attentional control and switching: this may explain why the magnitude of within-category decline was strongest in this condition. Whether within-category decline is maximised by a lack of availability of control resources is tested in Experiment 5. The current experiment also demonstrated a reduction in performance for both target and non-target trials (i.e., an increase in both misses and false alarms, see Appendix A). This result suggests that the within-category decline effect is not a change in participants' criteria for category membership. Instead it is more likely to occur because of an increasing inability to identify the targets and reject the non-targets.

Experiment 5: Effect of divided attention on within-category decline

Rationale

The magnitude of within-category decline in categorisation might be increased by a secondary task, which reduces the executive resources available for the semantic task. Research suggests that semantic cognition involves an interaction between conceptual representations and control processes that focus retrieval on currently-relevant aspects of knowledge (Jefferies, 2013; Lambon Ralph, Jefferies, Patterson, & Rogers, 2016). This type of control over retrieval may be partly achieved by domain-general executive mechanisms (although there might also be neurocognitive mechanisms that support semantic or memory control specifically; Davey et al., 2016; Noonan, Jefferies, Visser, & Ralph, 2013). Previous research has already shown that the requirement to perform a secondary task concurrently with semantic retrieval disrupts access to non-dominant knowledge (Almaghyuli, Thompson, Lambon Ralph, & Jefferies, 2012). Thus, if within-category decline reflects an increase in either competition or difficulty retrieving targets following longer-term weight changes, the application of control mechanisms that can resolve competition or promote weak but currently-relevant information should become more important towards the end of each category. Under these circumstances, the requirement to do two tasks at

once might have a particularly detrimental effect on comprehension towards the end of each category.

The neuropsychological literature already points to the importance of control processes since patients with semantic access deficits tend to have damage to left PFC and problems focussing retrieval on currently-relevant information that correlates with general executive dysfunction (Campanella et al., 2009; Gardner et al., 2012; Jefferies et al., 2007; Jefferies & Lambon Ralph, 2006; Schnur et al., 2009, 2006; Thompson et al., 2015). There are also several findings from the previous experiments reported here that suggest a role for control processes in within-category decline in categorisation. The interaction of within- and across-category decline seen in Experiment 3 but not the other experiments could have reflected the importance of executive resources for the difficult feature matching task, particularly at the end of each category (due to competition and/or weight changes), and a reduction in the capacity to apply executive control after sustained attention to a demanding feature-matching task. Within-category decline was also greater in the interleaved condition in Experiment 4, which required participants to switch between input modalities. The interleaved condition may have had higher control demands, reducing the executive resources available for maintaining the focus of semantic retrieval. To directly test the importance of executive resources, Experiment 5 examined within-category decline in the paced serial semantic task with and without the requirement to perform a secondary task.

Method

Participants: 24 undergraduate students (20 females and 4 males) from the University of York took part, in exchange for course credit or a payment of £5. The mean age of the students was 20 years (range of 18-30). All participants were native English speakers. All participants gave written informed consent.

Task Design: This experiment used a thematic category matching task (as for Experiment 1) and manipulated: (i) condition (single or dual), and (ii) strength of association (strongly vs. weakly associated targets). The effects of within-category and across-category decline were also examined. In the single task condition, participants were asked to press a button when they detected targets that related to the category (identical to Experiment 1). In the dual task condition, participants performed the same semantic task, except this time they were also asked to count triangles that appeared on the screen over the course of the category and report this number at the end.

Materials: All stimuli were taken from Experiment 1. Twenty thematic category labels were used (CHURCH, AIRPORT, MUSIC FESTIVAL, etc.) with 60 spoken items presented in each category. 20 items were related to the category, including 10 targets that were strongly related, (e.g., CHURCH – “priest”), and 10 that were distantly related to the category (e.g., CHURCH – “bread”) while the remaining 40 items were unrelated to the category (e.g. CHURCH – “oyster”) – these were recycled from other categories (see Appendix C for a complete list of items used). 10 categories were combined with the secondary task while 10 were presented under single task conditions. In the dual task condition, patterned triangles were presented on the screen (with 30 triangles appearing overall, 15 triangles distributed in the first half and 15 triangles in the second half of the session). In order to minimise the difficulty of the dual condition, only 2 – 4 triangles were presented per category, and these appeared on randomly-selected trials.

Procedure: Each session began with three practice blocks – the first block involved categorising spoken words (i.e. single task condition); the second block involved presentation of triangles (without any auditory stimuli), participants were asked to count the triangles that appeared from time to time on a blank screen and write down the number they had seen; the third practice block combined the two tasks. There were three categories with 30 trials (5 strongly related, 5 weakly related and 20 unrelated items) in each of the practice blocks. After the practice blocks, participants were presented with 20 experimental categories, using an ABBA or BAAB design for the single and dual-task conditions. The order of conditions, categories and items was fully counterbalanced between subjects.

Results

The results of Experiment 5 are presented in Figure 2.5. GLM analysis in this experiment included *secondary task condition* (single vs. dual task), *relatedness*, *across-category* and *within-category* as fixed within-subjects effects and included RT as a covariate. Parallel analysis using repeated-measures ANOVA on the sensitivity data indicated similar results (see Table 2.5 for *Wald* χ^2 , *F* and *p* values).

The analysis revealed significant main effects of secondary task condition (reduced sensitivity in the dual task compared to the single task), relatedness (lower sensitivity for the weak than strong targets) and a marginal main effect of across-category decline (sensitivity scores declined overall from the first half to the second half the session). There was no main effect of a within-category decline, but there was a significant interaction between relatedness and within-category performance: the decline in categorisation was greater for strong than weak items

towards the end of each category. This was supported by post-hoc tests with Bonferroni correction, that showed highly significant decline for strong items: $t(23) = 7.41, p < .001$, and near-significant decline for weak items: $t(23) = 1.99, p = .058$.

There was a trend-level three-way interaction between dual task condition, relatedness and within-category decline. This was explored by analysing performance for the strong and weak targets separately. The dual task by within-category interaction was significant for strong items: $t(23) = 2.83, p = .009$, but not for the weak items ($p > .1$). Other interactions were not significant ($p > .1$).

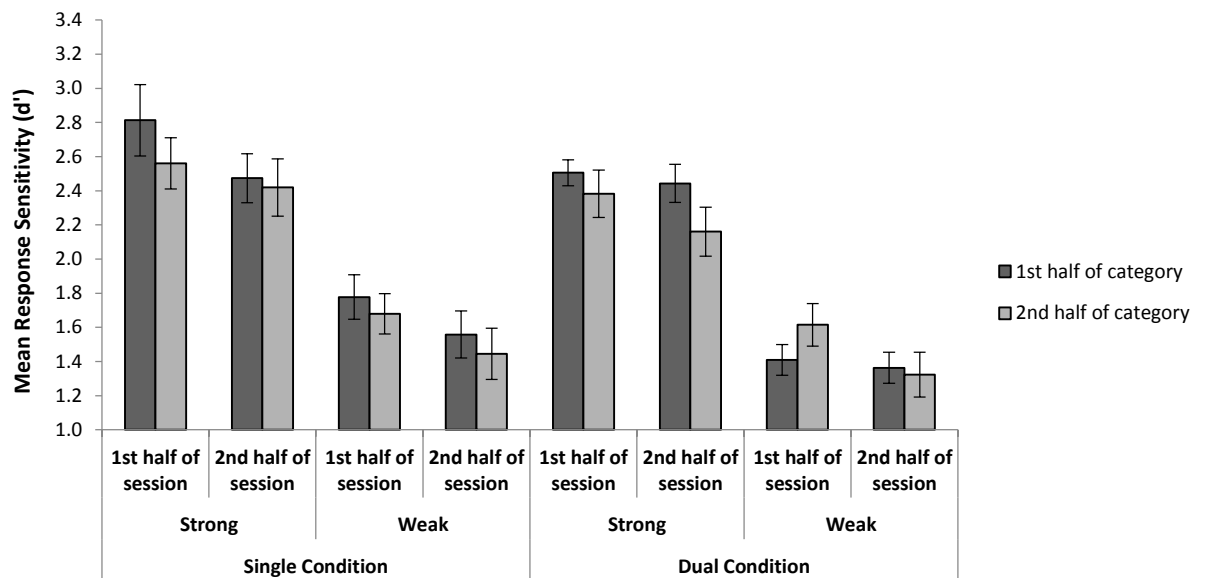


Figure 2.5: Mean response sensitivity (d') in Experiment 5 (Effect of divided attention), shown individually for the strong/weak targets, in the two conditions (single/dual), and split by first and second half of each category (within-category fatigue) and across the testing session (across-category fatigue). Error bars show SE of the mean.

Table 2.5: Summary of significant results for response sensitivity from GLM and repeated-measures ANOVA analysis, examining effects of condition (single/dual), relatedness, plus within-category changes in performance, in Experiment 5: Effect of divided attention.

Experiment 5: Divided attention			
		<i>GLM (RT covariate)</i>	<i>ANOVA</i>
Fixed effects:	<i>df</i>	<i>Wald χ^2, p</i>	<i>F, p</i>
Across-category	(1, 23)	<i>3.79, p = .052</i>	<i>2.52, p = .127</i>
Within-category	(1, 23)	<i>p > .1</i>	<i>p > .1</i>
Condition (single/dual)	(1, 23)	<i>6.81, p = .009</i>	<i>7.55, p = .012</i>
Relatedness	(1, 23)	<i>401.28, p < .001</i>	<i>327.25, p < .001</i>
Interactions:			
Relatedness x Within-category	(1, 23)	<i>6.60, p = .010</i>	<i>9.59, p = .005</i>
Condition x relatedness x within-category	(1, 23)	<i>3.55, p = .060</i>	<i>2.59, p = .123</i>

Footnote: Table presents two parallel analyses employing (i) mixed effects modelling (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) analysis of variance. Other interaction terms were non-significant ($p > .1$).

Summary of Experiment 5

The strong items showed a substantial effect of within-category decline, especially under dual task conditions; i.e., divided attention augmented within category decline. Thus, this experiment provides tentative support for the view that a reduction in executive control increases the effects of within-category decline. Executive resources might allow participants to selectively focus on the specific link between the category and each new target to prevent within category declines in comprehension.

Cross-experiment effects of within-category decline

In the final analysis, a meta-analysis was conducted of the magnitude of within-category decline (i.e., performance in the first and second half of each category) and across-category decline (i.e., performance in the first and second half of each experiment). In the first comparison all experiments employing a 1.1s presentation speed were included. This included the fast presentation condition of Experiment 1, Experiments 2 and 3, plus the single-task condition from Experiment 5. This analysis collapsed across strong and weak targets in Experiments 1 and 5.

GLM analysis included *across-category* and *within-category* as within-subjects fixed effects. *Experiment* was included as a between-subjects factor to establish if the magnitude of within- or across-category decline varied across these experiments. RT per condition and participant was again used as a covariate (see Table 2.6 for results).

There was a main effect of Experiment: the taxonomic categorisation task (Experiment 2) was easier than thematic matching (Experiment 1), specific feature matching (Experiment 3) and the single-task condition in Experiment 5. There was a significant main effect of within-category decline across these four experiments (see Figure 2.6). There was no main effect of a decline across-category and there were no significant interactions ($p > .1$). A decline in performance was revealed towards the end of each category across experiments. Effect sizes (Cohen's d) were also calculated to examine the standardised difference between experiment means, and have been summarised in Table 2.7. Effect sizes overall ranged from .09 to 1.02, with the effect of within-category decline being greatest in Experiment 2, and smallest in Experiment 5, in accordance with the results from the GLM.

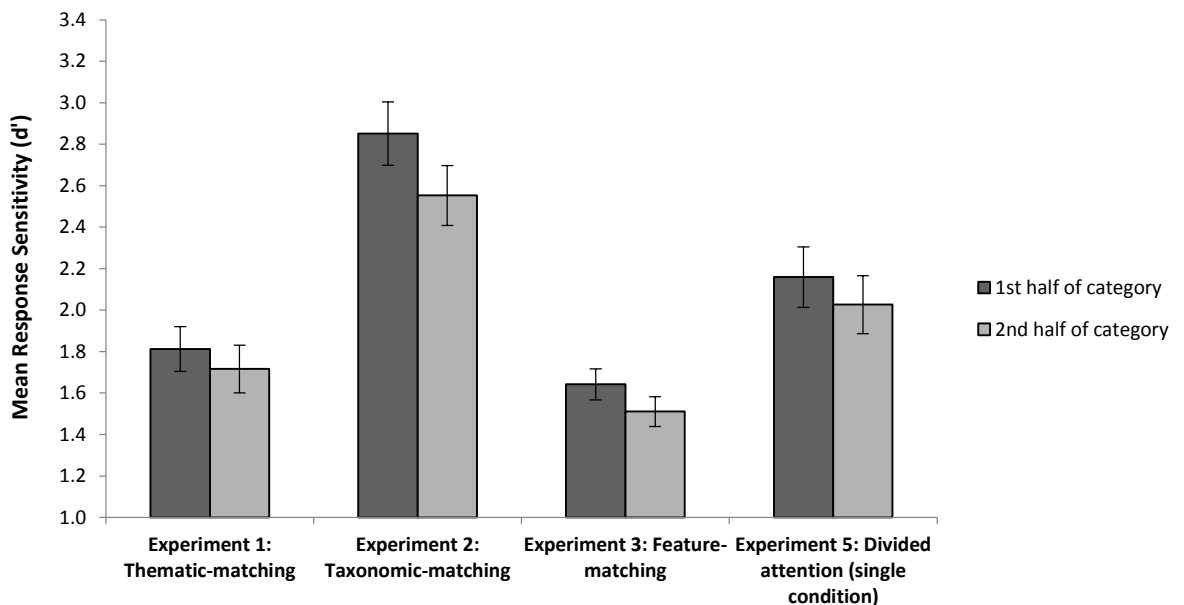


Figure 2.6: Mean response sensitivity (d'), shown individually for the first and second half of each category (within-category fatigue) and across the testing session (across-category fatigue), for Experiments 1, 2, 3 and 5 (single condition), at the presentation speed of 1.1 seconds. Error bars show SE of the mean.

Table 2.6: Summary of significant results from GLM and repeated-measures ANOVA analysis, examining across-category and within-category changes in performance across Experiments 1 (Thematic-matching), 2 (Taxonomic-matching), 3 (Feature-matching), and 5 (Effect of divided attention, single condition).

Cross-Experiment comparison			
		<i>GLM (RT covariate)</i>	<i>ANOVA</i>
Fixed effects:	<i>df</i>	Wald χ^2, <i>p</i>	<i>F</i>, <i>p</i>
Experiment	(1, 92)	72.64, <i>p</i> < .001	27.79, <i>p</i> < .001
Across-category	(1, 92)	<i>p</i> > .1	<i>p</i> > .1
Within-category	(1, 92)	15.53, <i>p</i> < .001	14.83, <i>p</i> < .001
Interactions (all <i>n.s.</i>):		<i>p</i> > .1	<i>p</i> > .1

Footnote: Table presents two parallel analyses employing (i) mixed effects modelling (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) analysis of variance. Experiment was included as a between-subjects factor.

Table 2.7: Effect sizes comparisons across the experiments included in the meta-analysis to examine within-category changes in performance, and performance based on relatedness.

Cross-experiment comparison - effect sizes		
	Effect of 'within-category' decline	Effect of relatedness
Experiment 1 (Thematic-matching)	0.48	0.13
Experiment 2 (Taxonomic-matching)	1.02	-
Experiment 3 (Feature-matching)	0.93	-
Experiment 4 (Words modality)	-	0.33
Experiment 5 (Divided attention)	0.09	0.4

Footnote: Effect sizes are evaluated with Cohen's *d*; effect sizes of .2, .5, and .8 are small, medium, and large, respectively (Cohen, 1988)

To further characterise the way in which performance changed across successive items within the categories, performance was examined for individual items, and the average number of hits and false alarms were computed for items in each position across experiments. There was a largely continuous decline in hits, with no substantial increase in false alarms (see Figure 2.7).

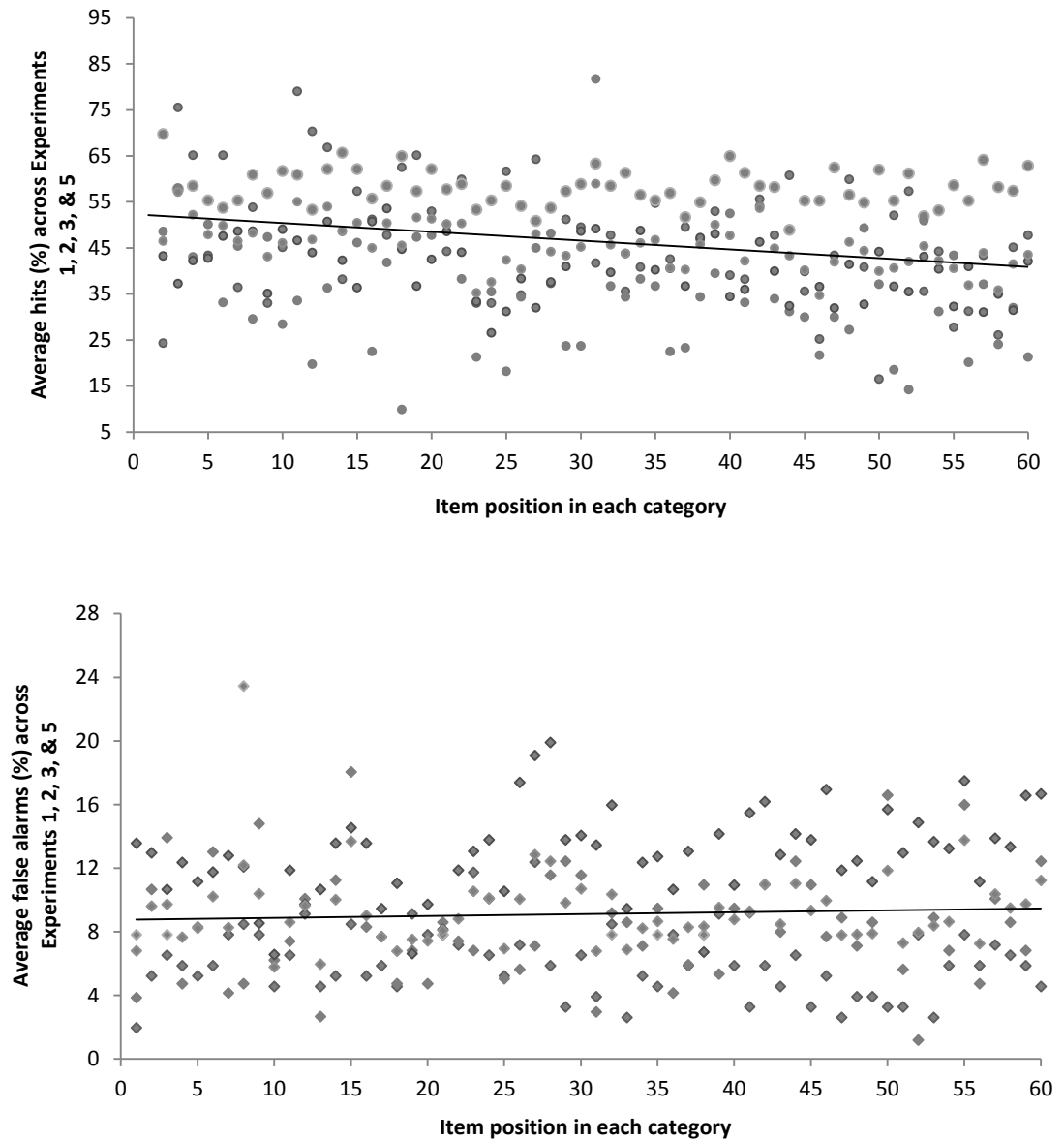


Figure 2.7: Average number of hits and false alarms for items within each category and across participants in Experiments 1 (Thematic-matching), 2 (Taxonomic-matching), 3 (Feature-matching) and 5 (Divided attention: single condition).

Cross-experiment effects of relatedness

Next, the relationship between within-category and the relatedness of targets across experiments was examined. Here data was included from Experiment 1 (strong vs. weak targets, collapsed across the two speeds – 2s and 1.1s), Experiment 4 (strong vs. weak word targets, collapsed across interleaved and non-interleaved conditions) and Experiment 5 (strong vs. weak targets, collapsed across the single and dual conditions). The picture condition from Experiment 4 was omitted since verbal measures of strength of association may not apply to picture-based decisions.

A GLM examining response sensitivity included *relatedness* and *within-category* as fixed effects within-subjects, *Experiment* as a between-subjects factor, and RT as a covariate (see Table 2.8 for results and parallel analysis using repeated-measures ANOVA). The analysis revealed a main effect of relatedness: overall sensitivity scores were lower for weak compared to strong targets (see Figure 2.8). There was a main effect of within-category decline: sensitivity declined towards the end of each category across the three experiments. Importantly, there was a significant interaction between relatedness and within-category decline. Post-hoc tests with Bonferroni correction indicated a significant within-category decline for strong targets across experiments: $t(69) = 3.83, p < .001$, but not weak associations ($p > .1$). Thus, performance declined more substantially for strongly than-weakly related targets across experiments.

There was also a significant interaction between task and relatedness: there was a stronger effect of relatedness in Experiment 5 (which involved divided attention) and in Experiment 4 (which involved interleaved presentation), in comparison to Experiment 1 (a simpler thematic matching task). Post-hoc tests with Bonferroni correction indicated a significant effect of relatedness in all experiments, which was largest in Experiment 5: $t(23) = 21.38, p < .001$, followed by Experiment 4: $t(21) = 8.28, p < .001$, and smallest in Experiment 1: $t(23) = 6.41, p < .001$. Since Experiments 4 and 5 had lower levels of sensitivity overall, the effects of strength of association appeared to be greater in more executively-demanding paradigms.

Lastly, effect sizes (Cohen's d) were also calculated, and have been summarised in Table 2.7. The overall effect sizes were small (effect sizes of .2, .5, and .8, are small, medium, and large, respectively; Cohen, 1988) and ranged from .13 to .40, with the effect of relatedness being greater in Experiment 5, and smallest in Experiment 1, also being in line with the GLM findings.

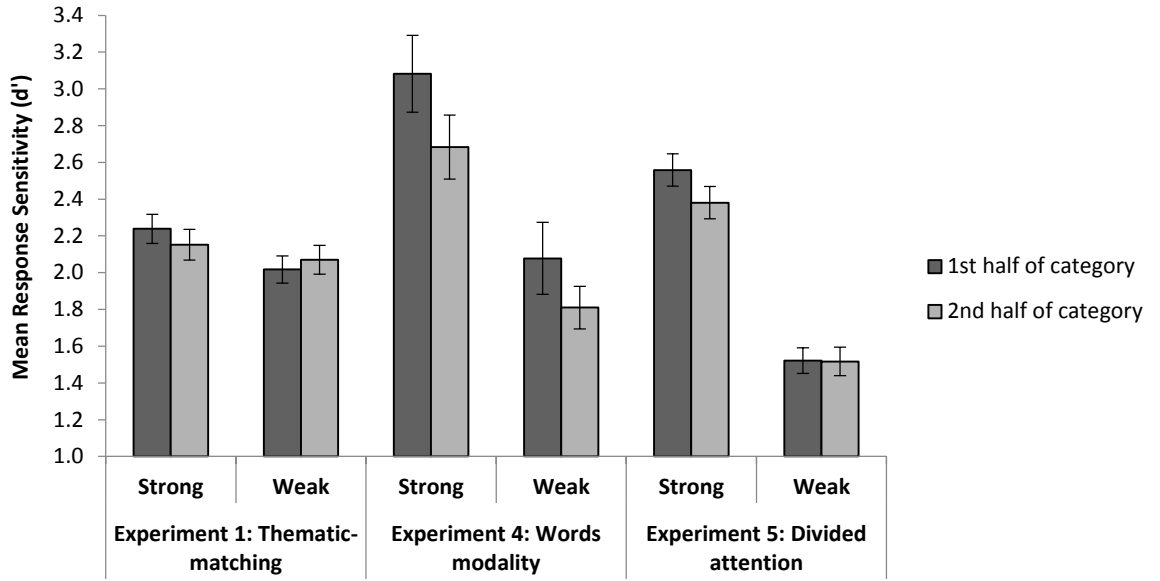


Figure 2.8: Mean response sensitivity (d'), shown individually for the first and second half of each category (within-category fatigue) and split by strong and weak trials, for Experiments 1, 4 and 5. Error bars show SE of the mean.

Table 2.8: Summary of significant results from GLM and repeated-measures ANOVA analysis, examining relatedness and within-category performance across Experiments 1 (Thematic-matching), 4 (Words modality), and 5 (Effect of divided attention).

	<i>df</i>	Cross-experiment relatedness comparison	
		GLM (RT covariate)	ANOVA
Fixed effects:			
Experiment	(1, 67)	6.83, $p = .033$	4.38, $p = .016$
Within-category	(1, 67)	7.16, $p = .007$	7.09, $p = .010$
Relatedness	(1, 67)	289.14, $p < .001$	299.72, $p < .001$
Interactions:			
Relatedness x Experiment	(1, 67)	265.26, $p < .001$	45.72, $p < .001$
Relatedness x Within-category	(1, 67)	10.83, $p = .001$	11.12, $p = .001$
Within-category x Experiment	(1, 67)	$p > .1$	2.84, $p = .066$

Footnote: Table presents two parallel analyses employing (i) mixed effects modelling (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) analysis of variance. Experiment was included as a between-subjects factor. Other interaction terms were non-significant ($p > .1$).

Discussion

Across five experiments, a cumulative decline in semantic categorisation was demonstrated as a consequence of sustained semantic retrieval, even in the absence of item repetition: participants' ability to detect targets belonging to a particular category deteriorated. This effect was not equivalent to time-on-task, and could not be explained as a general decline in sustained attention as a result of fatigue, since many categories were tested back-to-back over the course of the experiments and there was a release from this phenomenon at the category boundaries, when targets were no longer related to recently-categorised targets. The effects were observed in two different paradigms: both in a vigilance paradigm, in which participants attempted to detect targets that were less frequent than distracters, and also in a 2AFC paradigm, where target and distracter items within and outside of the target category were presented equally often. This confirmed that participants were less able to categorise accurately towards the end of each category, and were not simply changing their response criteria following more experience with each category. The effect was largest for targets *strongly* related to the category, supporting the suggestion that this phenomenon is semantic in origin. However, it did not require a global semantic relationship between the targets within the category: within-category decline was seen across taxonomic, thematic and individual feature-based classification, suggesting this pattern may be a fairly ubiquitous consequence of sustained semantic retrieval, at least in circumstances such as those created by the PSST paradigm, where the focus of retrieval is pre-defined and not permitted to evolve over time. The effect was also multimodal (extending to a paradigm in which semantically-related pictures and words were interleaved), confirming that it is conceptual in origin. Finally, it was increased by conditions of divided attention, suggesting that the capacity to maintain semantic retrieval within a category can be increased through the allocation of executive control.

Results add to a growing body of work showing that conceptual processing can become less efficient following the retrieval of semantically-related items. The within-category effect resembled both declining comprehension in patients with semantic access deficits (e.g., Gardner et al., 2012; Jefferies et al., 2007; Thompson et al., 2015; Warrington & Crutch, 2004), and similar effects seen in healthy participants when semantically-related items are categorised (Campanella & Shallice, 2011; Harvey & Schnur, 2015; Wei & Schnur, 2015) – however, it occurred *without* the massed repetition of individual items that was common across all of these studies. The paradigm resembled a continuous picture naming task, in which performance declines when semantically-related items are inter-mixed with fillers and presented in a sequence (Belke & Stielow, 2013;

Belke, 2013; Howard et al., 2006; Kleinman, 2013; Navarrete et al., 2010; Oppenheim et al., 2010; Runnqvist et al., 2012; Schnur, 2014). However, rather than requiring speech output, the task involved the comprehension and categorisation of meaningful inputs. Previous work using the continuous paradigm has found *facilitation* in categorisation (Belke, 2013; Riley et al., 2015), while this study found declining performance by adapting this paradigm to require more semantically-demanding decisions (cf. Wei & Schnur, 2015) and rapid responses (cf. Campanella & Shallice, 2011). Therefore, these findings have potentially important implications for understanding the mechanisms that support and shape sustained semantic retrieval and comprehension.

There has been considerable discussion of (i) whether cumulative interference occurs in comprehension paradigms as a result of processing semantically-related items (or whether these effects are restricted to picture naming); (ii) whether such effects arise at the level of lexical or semantic representations and (iii) whether these effects are short-lived (reflecting on-going activation of semantically-related items that produces interference), or are longer-lasting (reflecting weight-changes or adaptation within the underlying representations). First, the results add robust support to the hypothesis that semantic performance can decline as a consequence of the on-going processing of related concepts, since a similar pattern emerged across all five experiments. Secondly, within the literature on semantic access impairment, there has been debate about whether declining comprehension is restricted to auditory-verbal materials (Crutch & Warrington, 2008; Warrington & McCarthy, 1983; Warrington & Crutch, 2004), or whether it extends to non-verbal tasks (Forde & Humphreys, 1997; Gardner et al., 2012; Thompson et al., 2015). Similarly, opposing psycholinguistic studies have argued that semantic interference effects reflect lexical processes (e.g., Damian et al., 2001) or alternatively conceptual processes that extend to picture matching tasks (Wei & Schnur, 2015). It was reasoned that if these interference effects emerge from within modality-specific representations, within-category decline should be weaker in an 'interleaved' condition involving both words and pictures, as there would be more time for recovery between successive items, and/or fewer related targets presented within a modality to produce a decline in performance. In contrast, if these effects arise at a multi-modal conceptual level, they should be strong even when inputs of different modalities are interleaved. It was found that within-category declines in comprehension extended beyond auditory-verbal stimuli to include categories in which semantically-related word and picture stimuli were interleaved, suggesting that these results are unlikely to reflect either effects at a lexical-level or effects within the mappings between concepts and specific inputs (e.g., auditory word forms; structural descriptions of objects). Therefore, the second conclusion is that this phenomenon originated within amodal conceptual representations that are not specific to a particular input

modality (as envisaged by Patterson, Nestor, & Rogers, 2007; Rogers et al., 2004; see also Wei & Schnur, 2015).

Like semantic access deficits in patients with brain injury, the within-category decline in categorisation was sensitive to presentation rate: it was stronger when rapid processing was required. This resembles Campanella and Shallice's (2011) findings, which showed deteriorating comprehension for repeated items in semantically-related sets when healthy participants had to respond by a deadline. Sensitivity to speed of response suggests that this effect might reflect a process that takes time to resolve – such as narrowing the pattern of retrieval to focus on information relevant to the target. On the surface, the results are less compatible with the findings of Wei & Schnur (2015), who found rapid facilitation from semantic overlap with recent previous trials, plus longer-term inhibition (when semantically-related trials were presented at longer lags). However, the two paradigms are different in some important ways: the requirement to respond rapidly was contrasted with a condition in which there was more time for retrieval; however, the lag between successive targets was not manipulated and the cumulative decline in categorisation was unlikely to be very short-term since the targets were interspersed with distractors. Thus, it can be proposed that the observed effects are compatible with a build-up of conceptual interference (potentially over the medium-to-longer term, as reported by Wei & Schnur, 2015), combined with a retrieval process for each item that takes time to resolve, meaning that participants were less likely to settle on the correct response when there was little time to respond, following the build-up of conceptual interference towards the end of each category.

There was also some evidence across the set of experiments that within-category decline was greater when executive capacity was reduced. The effect was larger towards the end of more executively-demanding paradigms, such as the specific feature-matching judgements in Experiment 3, perhaps because participants were no longer able or willing to constrain semantic retrieval in an effortful way to meet the demands of the task. Similarly, within-category decline was greater in the interleaved condition of Experiment 4, which required greater attentional control to switch between words and pictures. Experiment 5 directly manipulated the availability of executive resources through the use of a secondary task to divide attention, and this appeared to increase the magnitude of the within-category decline in categorisation for highly-related items. Thus, it might be that the most substantial effects of within-category decline in categorisation occur when: (i) new targets are highly related to the specified goal for categorisation that have already been linked to other targets, and (ii) executive resources that could be used to control the negative effect of this previous retrieval are weak. In this way, the

results show an interaction between factors that load on distinct aspects of semantic cognition (Jefferies, 2013; Lambon Ralph et al., 2016): strength of association should influence the spread of activation to related concepts within the semantic store, while conditions of divided attention influence the extent to which retrieval can be controlled through the effortful allocation of attention to task-relevant semantic features. In this way, the findings are readily related to contemporary accounts of semantic processing, which envisage that amodal concepts interact with control processes to support context- and task-appropriate semantic retrieval.

The requirement in the paradigm to retrieve links between probes and *novel* target words is reminiscent of the “cue-overload effect” (Watkins & Watkins, 1975). Research on this phenomenon has shown that when many different associations to a given item are encoded or primed, this can interfere with the ability to recall each of these links, presumably due to the existence of many possible associations that can be retrieved from the cue (i.e., competition from primed or currently active representations) and/or following reductions in the efficiency with which the cue can activate the current target (i.e., following the retrieval-induced forgetting initiated by the earlier retrieval of related targets). The PSST paradigm characterises the *immediate* effects of previous retrieval on evolving performance, as opposed to the subsequent effects of having many activated associations during later recall. Towards the end of each category, when performance was poorer, there may have been more interference with the classification of new targets, following the priming of other goal-relevant representations (reflecting residual activation of previous targets or, perhaps more likely given the nature of the task, weight changes between the category goal and previous targets). This made it more difficult to identify the relationship between a newly-presented item and the target category (especially when there was a short deadline to respond). For example, for the category PICNIC, previous targets “sunshine” and “rug” might have made the categorisation of a new item, “cake”, less efficient, since these items would have been previously associated with the goal and all of the items shared goal-relevant features; thus there may have been competition at the point of decision. This might explain why a greater disruption was found for targets highly coherent with the goal (i.e., for targets that were strongly associated with the goal category). However, global similarity between the different targets was not essential for the within-category decline effect, since it was maintained in the feature-based task (i.e., the category RED), when target concepts shared few features besides the property specified by the current category. This suggests that it was overlap between the successive items and the goal feature that was critical for interference with subsequent semantic retrieval or decision making.

A number of alternative explanations of the within-category decline can be ruled out: (i) it did not result from satiation or competition at the level of lexical-semantic representations or links between a specific input modality and conceptual knowledge. The effect did not require the same inputs to be presented multiple times; moreover, the effects were larger in an experiment in which spoken words and pictures were interleaved. (ii) The effect did not result from participants adjusting their working definition of the category over the set of trials, since Experiment 4, which required a response to each item, revealed that both false alarms and misses increased over this period. Thus, there was no evidence that people loosened the category boundaries as they learned about the weak items (increasing false alarms specifically), or tightened the category boundaries as they encountered more strong items (increasing misses specifically). (iii) The effect cannot be explained in terms of diminished executive resources per se: although the effect was increased by a secondary task and interacted with time-on-task, it was greater for high-association items that are easier, and was not *equivalent* to time-on-task.

The phenomenon described in this study would tend to promote an evolving pattern of retrieval that does not stay focussed on the same tight category but changes over time. Interestingly, this phenomenon is seen commonly in patterns of semantic retrieval that occur in everyday life, such as during mind-wandering and when conversations spontaneously shift topic (e.g., Humphries, Binder, Medler, & Liebenthal, 2006). This work suggests that a sustained focus of retrieval on one topic might require executive resources since activation within the semantic system will spread more and more broadly to irrelevant features and associations automatically. In the real world, it might only be a matter of time before one of these alternative avenues becomes the focus of our retrieval.

Chapter 3

Semantic control deficits and retrieval-induced changes in categorisation: Evidence from ageing and semantic aphasia

Acknowledgements: Assistance with collecting data from stroke patients was provided by Hannah Thompson. Part of the data collection with age-matched controls was by Dominic Arnold and Woody Chau for a summer bursary project. Assistance with collecting background neuropsychological data from patients was provided by Glyn Hallam and Sara Stampacchia.

Abstract

Patients with semantic aphasia following prefrontal or temporoparietal stroke have difficulty controlling activation within the semantic system, and accessing appropriate knowledge for a given task or context. These patients show “refractory effects” – i.e., declining accuracy in cyclical word-picture matching tasks when semantically-related sets are presented rapidly and repeatedly. A similar decline in comprehension in healthy young adults was observed in the previous chapter, even without the repetition of individual items, using a paced serial semantic task (PSST). This chapter considers how ageing and semantic aphasia influence within-category decline in categorisation on this task. It was reasoned that if within-category decline in categorisation reflects difficulty selecting currently-relevant knowledge in the face of growing competition, patients with semantic aphasia and older adults might show this effect more strongly, if their capacity to control semantic retrieval is compromised. In contrast, if the effect arises from the suppression of competitors during categorisation on earlier trials, participants who are less able to control interference in this way should show an attenuation of this decline in categorisation. The results showed that both patients with SA (relative to age-matched controls) and older adults (relative to younger adults) were less efficient at retrieving weak associations, relative to stronger ones: in this way, both groups appeared to have weakened controlled retrieval of semantic information. Older adults and SA patients showed little within-category decline, unlike young adults, suggesting this effect reflects retrieval-induced forgetting following the application of control to reduce semantic interference on earlier trials. The PSST was also used to examine the contribution of post-stroke fatigue to sustained attention and cognitive impairment in aphasia, using a fatigue visual analogue scale (F-VAS) to assess the subjective feeling of fatigue at different time points during PSST testing. Some patients showed an overall pattern of declining comprehension over the session, which correlated with their subjective feelings of fatigue. However, semantic control deficits and fatigue were independent in patients in this study. Therefore, fatigue in aphasia post-stroke is not likely to be a consequence of the increased effort required for sustained language processing.

Introduction

The previous chapter showed declining comprehension in healthy young adults in the PSST, even without repetition of individual items, and a release from this effect at category boundaries. These findings suggest that it becomes progressively harder to maintain focussed semantic retrieval on a single topic – which might explain why it can be hard to sustain attention to the central theme of written or spoken language in everyday situations. Within-category decline in young adults was found to be greater for strong associations, suggesting this effect may be underpinned by building competition or retrieval-induced inhibition between highly related items. This decline was also increased by a secondary task that divided attention, suggesting that control may be employed to overcome the effects of strong but task-irrelevant activation for related items, or the effects of retrieval-induced forgetting. This chapter considers how ageing and semantic aphasia may influence declining performance on the PSST paradigm, since the capacity to employ semantic control to tailor semantic retrieval to a specific goal may be compromised in patients with semantic control deficits and may also be weaker in older adults relative to younger volunteers. This would enable us to examine the following two predictions: (i) People with weaker control may show an *increased* effect of within-category decline, as they are less able to overcome increasing competition from earlier trials. (ii) Alternatively, they may show *reduced* effect of within-category decline, if this effect reflects suppression of related information during earlier categorisation. Thus, performance in this group should speak to the mechanisms that underpin this effect.

Older adults continue to acquire conceptual information over the lifespan, and tests of semantic knowledge do not show the marked age-related declines seen for episodic and working memory (Cabeza et al., 2004; Haut, Chen, & Edwards, 1999; Mitchell, Johnson, Raye, Mather, & D’Esposito, 2000). However, since semantic cognition is thought to emerge from the interaction of multiple neurocognitive components, including the conceptual store in the anterior temporal lobes (ATL) and control processes that shape semantic retrieval in left prefrontal cortex (Jefferies, 2013; Noonan, Jefferies, Visser, & Ralph, 2013), some aspects of semantic cognition may show greater age-related cognitive decline than others. In particular, the *retrieval* of semantic information may be more vulnerable in ageing than the retention of knowledge itself. Older adults take longer to retrieve information from memory (Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, Bernstein, Beig, & Siegenthaler, 2002; Gutchess et al., 2005; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Madden et al., 1999; Morcom, Good, Frackowiak, & Rugg, 2003; Öztekin, Güngör, & Badre, 2012; Rosen et al., 2002) and this slowing might reflect a

reduced spread of activity through semantic representations, or difficulty focussing this activity on the target, or both.

The frontal lobe theory of ageing proposes that many age-related changes in cognition are due to the vulnerability of the frontal lobes to structural and neurochemical changes that occur in older adults (Buckner, 2004; Raz et al., 1997; West, 1996). Poorer performance has been observed in healthy elderly participants on clinical tests of frontal lobe function such as the Wisconsin Card Sorting Test and the Trail Making Test (Fristoe, Salthouse, & Woodard, 1997; Libon et al., 1994). Since semantic cognition draws on domain-general executive mechanisms, older adults might be expected to have difficulties on harder semantic tasks, for example, when retrieval has to be focussed on specific non-dominant features required by the task. However, research suggests that the neurocognitive mechanisms underpinning semantic and executive control are partially distinct (Davey et al., 2016), and so it is not yet clear if poorer performance on executive tasks will extend to semantic tasks in older adults. If older adults have impaired semantic control relative to younger adults – i.e., if they are less able to flexibly focus retrieval on the aspects of knowledge that are relevant for the task or context – they may have particular difficulty detecting the relationship between category labels and *weak* targets on the PSST, since understanding the relevance of weak semantic associations is thought to require stronger engagement of controlled retrieval mechanisms (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001).

In addition, the progressive loss of frontal activity is also known to affect inhibitory mechanisms, particularly on the influence of irrelevant responses or material (Garavan, Ross, Li, & Stein, 2000), i.e., older adults are less able to suppress irrelevant or distracting information (Lustig, Hasher, & Zacks, 2007). Similarly, studies on regions that index 'default-mode' activity, i.e., when people attend to an internal based focus rather to an external task focus (Gusnard & Raichle, 2001; Raichle et al., 2001), have provided further evidence that ageing can impact decreased inhibition or the capacity to appropriately engage attention. Activity in default-mode regions has been shown to decrease, relative to rest periods, in both auditory tasks (Alain, Arnott, Hevenor, Graham, & Grady, 2001) and visual tasks (Haxby et al., 1994; Shulman et al., 1997). Several studies have reported that default-mode activity in healthy older adults during task performance is not reduced to the same extent as seen in younger adults (Greicius et al., 2004; Lustig et al., 2003). Furthermore, recent studies have reported that lower levels of control enable older adults to encode more information compared to younger adults (Campbell, Hasher, & Thomas, 2010; see also Rowe, Valderrama, Hasher, & Lenartowicz, 2006). For example, older

adults showed increased priming effects of distractors than younger adults, and this benefitted their later performance on the task, i.e., older adults were able to use distracting information from previous trials that younger adults had inhibited (Amer & Hasher, 2014; Biss, Ngo, Hasher, Campbell, & Rowe, 2013). Therefore, if retrieving relevant information after it has been inhibited on earlier trials is likely to draw more strongly on control process on the PSST, then earlier trials may trigger less suppression of related information in older adults, and thus the effect of within-category decline may be eliminated or attenuated with ageing.

This study also investigated semantic cognition in patients with semantic aphasia using the same paradigm. These patients have multimodal semantic deficits associated with damage to left prefrontal and/or temporoparietal areas consequent to stroke (Jefferies & Lambon Ralph, 2006; Warrington & McCarthy, 1983; Warrington & Shallice, 1979). Previous work has suggested that SA patients have difficulty making connections between items that are further apart in semantic space (e.g., *chipmunk* with *bee*) than between more similar items (*chipmunk* with *squirrel*; Noonan et al., 2010). Therefore, SA patients can retain conceptual information but have deficits in retrieving it in an appropriate way for the task or context. They also show difficulty when non-dominant semantic features or associations are required and strong but irrelevant aspects of knowledge must be suppressed (Noonan, Jefferies, Corbett, & Lambon Ralph, 2010). Thus, depending on the mechanisms underpinning the within-category decline in categorisation, different effects would be expected, i.e., it is possible that SA patients may benefit on later trials if their initial retrieval is uncontrolled, i.e., eliminating the possibility of a within-category decline, or their performance would decline over the course of the category if the effects observed in Chapter 2 are a consequence of growing competition.

Intriguingly and highly relevant for this study, SA patients are reported to show 'refractory' effects on cyclical matching tasks – i.e., declining comprehension when items are presented repeatedly (Gardner et al., 2012; Jefferies, Baker, Doran, & Ralph, 2007; Thompson, Robson, Lambon Ralph, & Jefferies, 2015). In this paradigm, a probe item must be matched with one of four responses that are semantically related. The same response options are presented on every trial, but the target cycles round such that the item to-be-selected on one trial becomes the distractor on another (Cipolotti & Warrington, 1996; Warrington & McCarthy, 1983; Warrington & McCarthy, 1987). With multiple repetitions, patients are no longer able to match items which they correctly identified at the beginning of the block (Cipolotti & Warrington, 1996; Forde & Humphreys, 1995; Gardner et al., 2012; Jefferies et al., 2007; Schnur, Schwartz, Brecher, &

Hodgson, 2006; Schnur et al., 2009; Warrington & Crutch, 2004; Warrington & McCarthy, 1987). At a change of category, performance is restored (Gardner et al., 2012).

It has been argued that this refractory impairment may reflect difficulty overcoming competition that occurs when previously-selected items become distracters, and/or in updating goals such that the current target is the focus of selection (Damian, Vigliocco, & Levelt, 2001; Schnur et al., 2006). However, it is unclear whether 'refractory effects' are linked to the difficulty of sustaining a specific focus for semantic retrieval (e.g., whether such patients would also show within-category decline on the PSST). It is also unclear whether this deterioration in comprehension over repeated trials is connected to cognitive fatigue more generally. Many people with post-stroke aphasia experience cognitive fatigue – i.e., a sense of exhaustion after effortful language, cognitive and/or social processing – and this which can be debilitating even for stroke survivors who have otherwise made a full recovery (Staub & Bogousslavsky, 2001). The relationship between fatigue and aphasia has rarely been examined, yet the capacity to maintain a central focus for semantic cognition could be related to this difficulty.

The PSST paradigm from Chapter 2 (Experiment 1: Thematic-matching) was used, to examine performance in older adults and SA patients, as this allowed to characterise changes in semantic cognition in these groups in terms of: (1) the effect of strength of association (strong vs. weakly-related targets); (2) within-category decline – e.g., increasing problems categorising inputs when a large field of related information has already been activated and yet a specific focus has to be maintained; (3) across-category decline – e.g., general cognitive fatigue which might produce deteriorating performance on the paradigm over the course of each testing session. It was hypothesised that older adults and patients with semantic aphasia might both show reduced flexibility in semantic cognition, such that they would be disproportionately impaired at retrieving weak associations (although this effect was expected to be considerably more pronounced in patients). Furthermore, as within-category decline was found to reflect difficulty maintaining efficient categorisation in the face of building competition or retrieval-induced inhibition; it is possible that it might be impaired in patients with semantic aphasia who have deficits of semantic control, and potentially also in older adults who might also have less controlled semantic retrieval. However, an alternative hypothesis is also possible: these groups might show *reduced* within-category decline, relative to younger adults, if this effect does not simply follow from the build-up of competition following earlier retrieval, but reflects a more active process of resolving competition through the suppression of associated memories. In other words, patients with SA

and to some extent older adults may not deal with the demands of initial retrieval by suppressing competitors, and this may make them less vulnerable to within-category decline.

Methods

Participants

Older controls: Fifteen older adults, with a mean age of 73 years (SD = 8.1; range 55-84 years) were selected from a participant database at the University of York (ten female, five male). They were selected to provide an age-matched control group for the patient sample below.

Participants had no prior history of brain injury, and showed unimpaired cognitive functioning on the Mini-Mental State Examination (Folstein, Folstein, & McHugh, 1975), see Table 3.1 for their average performance on background semantic and executive assessments. They left school or college aged 18 (SD = 3.9 years).

SA patients: Twelve stroke aphasic patients (eight female, four male) were recruited from stroke clubs and speech and language therapy services in York and Leeds, UK. All patients had chronic impairment after a CVA at least one year prior to testing. Patients were aged between 40 and 78, with a mean age of 62 years (SD = 10.2). CT/MRI scans were available for eleven patients (see Figure 3.1). The patients were selected to show multimodal semantic impairment. Importantly, they were not selected to show declining comprehension or fatigue, allowing us to assess how common these patterns are in patients with aphasia following left-hemisphere stroke. Six patients were milder than those previously described, and so were not below the normal cut-off on the Camel and Cactus Test (see Table 3.1). Nonetheless, all cases were impaired at more demanding tests involving ambiguous words (verbal semantic test, Noonan et al., 2010), and matching pictures of objects to unusual uses (non-verbal semantic test, Corbett, Jefferies, & Ralph, 2011).

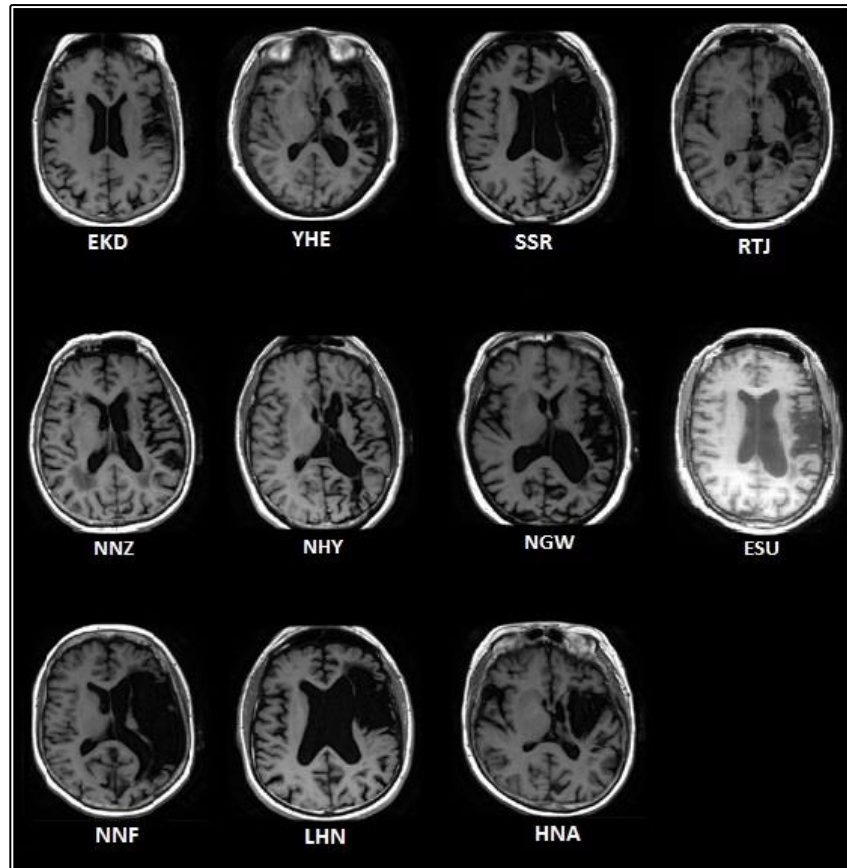


Figure 3.1: CT/MRI scans for the SA patients, arranged according to their semantic performance, from high to low.

Background testing

The patients were examined on neuropsychological tests to assess cognitive abilities. The following semantic and executive background assessments were used:

1. **Semantic assessments** included two components of the 64-item semantic test battery (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000):
 - (i) Spoken word-picture matching (WPM), involved matching a spoken word (e.g., “fork”) with a picture of the same item (e.g., FORK, SPOON, SPATULA, or KNIFE). The target was presented with ten semantically related distractors, as black and white line drawings.
 - (ii) The Camel and Cactus Task (CCT) – assessed using both picture (CCTp) and word (CCTw) versions. This test of semantic association involves deciding which of four semantically-related items has an association to a probe (e.g., does CAMEL go with CACTUS, TREE, SUNFLOWER, OR ROSE).
 - (iii) Additionally, a 96-item synonym judgement task, from Jefferies et al. (2009), involved matching a probe to a target word with the same meaning, presented with two unrelated distractors, for example: MONEY with CASH, CAR or CHURCH. Responses were untimed.

(iv) Faye's object use (Corbett et al., 2011) assessed non-verbal semantic control. Table 3.1 shows performance on these assessments for each patient. Factor analysis was used to extract one composite semantic score from word-picture matching, CCTp, CCTw and synonym judgement, with larger values representing better performance (see Table 3.5).

2. **Executive assessments:** (i) Trail making: this task involved linking letters and numbers in order, in an easy condition (e.g., 1-2-3...) and difficult condition (e.g., 1-A-2B-3-C...; Reitan, 1958). (ii) The Ravens Coloured Progressive Matrices test (RCPM: Raven, 1962) assessed non-verbal reasoning. (iii) The Brixton Spatial Rule Attainment task (BSRA: Burgess & Shallice, 1997), involved adapting patterns of responses based on feedback (see Table 3.1 for background assessment for each patient). Factor analysis was used to compute a composite executive score (see Table 3.5). The composite semantic and executive scores were highly correlated: $r = .650$, $p = .022$ (see Table 3.7).

3. **'Refractory' assessments:** A cyclical word-picture matching task was run using E-prime, and required patients to point to one of four pictures that depicted a spoken word. The items were presented in semantically-related sets and the items were presented repeatedly, such that the target on one trial became the distractor on another, until all four items within a semantic category had been the target. This completed one cycle. There were four cycles for each set of items, which probed the items in the semantic array in a pseudorandom order. The probe word was presented through speakers at the same time the four response pictures were presented on the screen. Patients indicated their response by pointing to one of the pictures and the experimenter pressed a key, which advanced the task onto the next trial. The experimenter recorded accuracy, whereas RT was recorded by the computer. As soon as a response was given, the next trial was presented. Each participant had 10 seconds to respond, and if they did not respond within this time, the next trial was presented and an error was recorded (results are shown in Table 3.4 and Figure 3.11).

Table 3.1: Background neuropsychological data for each patient and average control performance

	Max score	Control mean	Cut-off	EKD	ONY	YHE	SSR	RTJ	NNZ	NHY	NGW	ESU	NNF	LHN	HNA
Semantic tasks:															
WPM	64	60	63	64	63	62*	52*	63	64	62*	64	62*	60*	62*	63
CCT pictures	64	59	53	58	60	61	54	61	53	57	56	45*	45*	44*	31*
CCT words	64	61	57	63	58	60	57	56*	61	52*	53*	59	29*	43*	39*
Synonym Judgement	96	95	91	90*	87*	81*	87*	81*	78*	76*	74*	66*	71*	59*	57*
Object use: canonical	37	36	34	NA	36	37	33*	37	37	35	35	37	29*	31*	32*
Object use: non-canonical	37	34	29	NA	32	29	22*	32	26*	22*	21*	34	14*	13*	14*
Ambiguity: cues	60	60	59	NA	52*	54*	47*	57*	50*	51*	40*	43*	39*	35*	46*
Ambiguity: miscues	60	59	57	NA	50*	45*	39*	54*	42*	34*	22*	30*	27*	23*	19*
Executive tasks:															
Trail making	23	23	17	23	23	22	23	21	19	5*	12*	1*	16*	23	2*
RCPM	36	33	28	32	29	33	34	33	21*	30	24*	19*	31	29	31
BSRA	54	33	28	39	45	30	31	39	31	23*	26*	24*	18*	7*	21*
Phonological deficits:															
Cookie theft WPM		NA		NA	58	37	0*	38	54	37	12	60	9	18	0*
PALPA - repetition	80	NA	73	NA	NA	77	1*	7*	74	79	75	78	42*	71	0*

* Denotes impaired performance. NA = not available. Patients are arranged according to composite semantic severity scores; this is a single factor extracted from WPM = word picture matching, CCT = Camel and Cactus Task (both from Bozeat et al., 2000), and synonym judgement. RCPM = Raven's Coloured Progressive Matrices (Raven, 1962). BSRA = Brixton Spatial Attainment Task (Burgess & Shallice, 1997). PALPA = Psycholinguistic Assessments of Language Processing in Aphasia (Kay, Lesser, & Coltheart, 1992). Cookie theft description assesses fluency (words-per-minute; Goodglass & Kaplan, 1983).

Task and Design

The 'Paced Serial Semantic Task' or PSST requires rapid and continuous semantic association judgements that link spoken words to a thematic category, such as PICNIC or HOSPITAL. Participants were asked to classify spoken words in terms of whether they were associated with these categories or not.

Materials: Twenty different category labels were used (such as PICNIC) with 60 items in each category. 20 items were related to the category, including 10 targets that were strongly related to the category label, such as "*sandwich*"; and 10 that were distantly related, such as "*wasp*", while the remaining 40 items were unrelated to the category (e.g. "*exam*") – these were recycled items from other categories. Target words were selected using the Edinburgh Associative Thesaurus (EAT; Kiss, Armstrong, & Milroy, 1973), supplemented by a pilot study in which ratings were collected for the relatedness of each word to the category label. Participants (N = 16) used a 7-point Likert scale to judge relatedness, and items were categorised as strongly related (> 5.5), weakly related (2.2 - 5.5) or unrelated (< 2.2). (See Appendix C for a complete list of categories and items used).

Procedure: The experiment was presented using E-Prime 2.0 (Psychology Software Tools, Sharpsburg, PA). Testing was completed across two sessions. Category names were presented as written words that remained visible throughout the block, to reduce demands on working memory. Participants were asked to press a button each time they heard a word that was related to the category, and not to press for unrelated words. Before starting the experiment, patients were asked to rate their feelings of tiredness on a fatigue visual analogue scale (F-VAS; 0 being 'not at all tired' to 10 'extremely fatigued', see Figure 3.2). The session then continued with 20 minutes of PSST testing (i.e. 5 categories out of the 20) at a presentation speed of 2 seconds. This was followed by 15 minutes of neuropsychological testing. Participants were asked to rate their tiredness on the F-VAS before completing another 20 minutes of PSST testing (next 5 categories). The session concluded with a final rating of tiredness on the F-VAS. The remaining 10 categories were presented in the second session, which followed the same procedure.

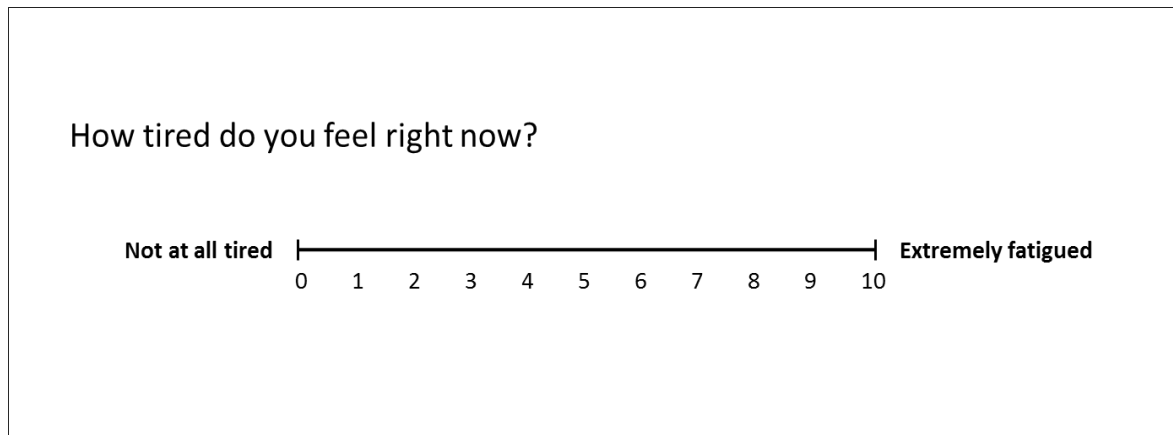


Figure 3.2: The fatigue visual analogue scale (F-VAS) used during PSST testing, patients were asked to circle a number based on their levels of tiredness at different time points during the session (0 – ‘not at all tired’ to 10 – ‘extremely fatigued’).

Results

The main dependent measure was response sensitivity (d'), since this study aimed to evaluate the effect of ageing and stroke aphasia on the ability to detect targets belonging to each category, by the deadline imposed by the task. For completeness, response time data is also presented.

This study used generalised linear models (GLMs) for all analyses and RT was entered as a covariate (i.e., the average speed for correct responses per condition per participant) in the analyses examining response sensitivity. Results are presented in three sections – the first section examines healthy individuals, comparing performance of the older controls with younger participants from the previous chapter to investigate possible differences in performance based on age. The second section examines SA patients in comparison to the age-matched controls; and the last section assesses individual differences in the SA patients, in relation to their semantic/executive deficits, fatigue ratings and performance on cyclical word-picture matching task that induce ‘refractory’ effects in patients with semantic aphasia (Gardner et al., 2012; Jefferies et al., 2007; Forde & Humphreys, 1997; Thompson-Schill, Hsu, & Schlichting, 2013; Warrington & Crutch, 2004).

1. Older vs. younger healthy adults

This comparison of younger and older adults employed the data from undergraduate volunteers tested in Chapter 2, Experiment 1 (thematic matching). Older adults were presented with the same stimuli using a presentation speed of one item every 2 seconds and only data from

this speed were included for the undergraduate group (Experiment 1 in Chapter 2 also included a 1.1s presentation speed condition but this was excluded from the analysis below). There were some other important methodological differences between the groups: 24 undergraduates performed two blocks of 5 categories at the speed of 2 seconds that were interspersed with two blocks of 5 categories at the speed of 1.1 seconds, in an ABBA or BAAB design (20 categories in total). In contrast, 15 older adults completed 10 categories across two sessions (on different days), with a break after the first 5 categories in each session, during which they performed background neuropsychological testing, to keep the testing format consistent with patients. To remove effects of these differences, performance was only assessed on the first 5 categories in both age groups, and therefore the potential effects of across-category decline were not examined. The analysis below also only includes data from the 12 younger participants who were tested on the 2 seconds speed first. However, supplementary analysis including all 24 younger volunteers reproduced the same findings (results are reported in Appendix B).

As responses were only required on 'yes' trials, the sensitivity (d') or response bias of the participants (the general tendency to respond *yes* or *no*; Stanislaw & Todorov, 1999) was examined. Higher d' scores reflect better response sensitivity (e.g., the ability to correctly recognise targets and reject distractors). GLMs were used to analyse average response sensitivity (shown in Figure 3.3), for each condition and for each participant, including within-subject fixed-effects of *relatedness* (strongly or weakly related targets to category) and *within-category* position (first vs. second half of each category), in a fully-factorial model that included all interaction terms for these predictor variables. *Group* (older vs. younger participants) was included as a between-subjects factor, and RT per condition and participant was used as a covariate. Similar model was used with RT data (see Table 3.2 for all *Wald* χ^2 and *p* values). Performance across all three measures has been discussed separately for the two main factors – (1) relatedness and (2) within-category performance.

Table 3.2: Summary of significant results from the GLM analysis for the age comparisons – looking at the effects of group, relatedness and within-category performance, for the key dependent measures - response sensitivity and response times.

Older vs. younger adults		
	<i>Response Sensitivity</i>	<i>Response Times</i>
Fixed effects:	Wald χ^2, <i>p</i>	Wald χ^2, <i>p</i>
Group	29.53, < .001	<i>p</i> > .1
Relatedness	36.03, < .001	301.45, < .001
Within-category	<i>p</i> > .1	10.827, .001
Interactions:		
Group x Relatedness	24.51, < .001	25.48, < .001
Group x Within-category	<i>p</i> > .1	3.26, <i>p</i> = .071
Group x Relatedness x Within-category	<i>p</i> > .1	<i>p</i> > .1

Footnote: Table presents analyses employing (i) mixed effects modelling for response sensitivity (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest), and (ii) mixed effects modelling for response times (i.e., GLM preserving performance information for each category for each participant).

(1) Relatedness

The main effect of relatedness was significant across the dependent measures (see Table 3.2 for *Wald χ^2* and *p* values). Response sensitivity elicited a significant interaction between *group* and *relatedness*: older adults showed a larger effect of relatedness than younger adults (see Figure 3.3). Individual GLMs were also used on the groups separately. The main effect of relatedness was significant in both groups, but was more marked in the older group: *Wald χ^2 (1) = 133.48, *p* < .001*, compared to the undergraduates: *Wald χ^2 (1) = 25.84, *p* < .001*.

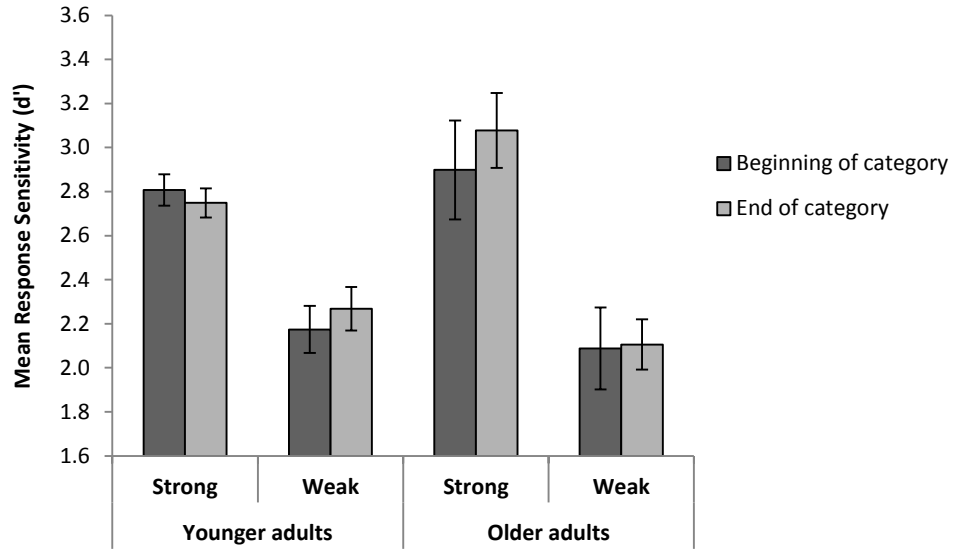


Figure 3.3: Mean response sensitivity (d') for the first and second half of each category (within-category performance), split by strong and weak targets for the two age groups. Error bars show *SE* of the mean.

The RT model also revealed a significant interaction between *group* and *relatedness*: both groups responded more slowly for weaker targets in comparison to strong targets, but this effect was substantially greater in older volunteers (see Figure 3.4). Individual GLM analysis found a relatedness effect in the older group: $Wald \chi^2(1) = 470.58, p < .001$, and younger group: $Wald \chi^2(1) = 99.32, p < .001$.

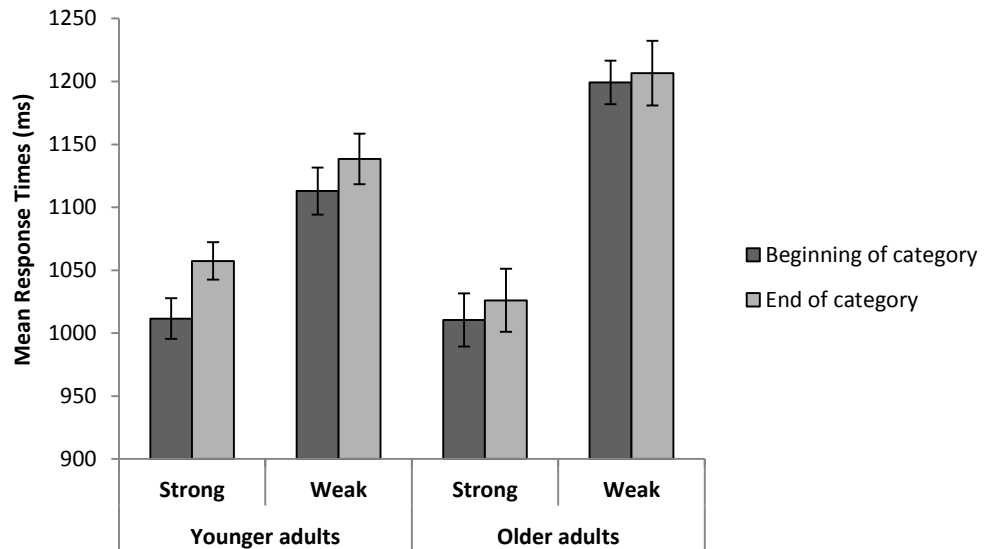


Figure 3.4: Mean response times (ms) for the first and second half of each category (within-category performance), split by strong and weak targets for the two age groups. Error bars show *SE* of the mean.

(2) Within-category performance

The main effect of within-category performance was only significant in the RT model (see Table 3.2 for *Wald* χ^2 and *p* values). There was a marginally-significant interaction between *group* and *within-category* change in performance in response times: participants made slower responses towards the end of each category (see Figure 3.4), and this increase in response times for successive targets within a category was significant in the younger participants: *Wald* $\chi^2(1) = 20.814$, $p < .001$, and not significant for older adults: *Wald* $\chi^2(1) = 1.26$, $p = .261$.

Interim summary

Older adults were more accurate than younger undergraduates, and showed equivalent response times. However, they showed greater difficulty with identifying weak associations, in both sensitivity and RT. These effects resembled the effect of the secondary task in Experiment 5 in Chapter 2, and could reflect poorer semantic control in older volunteers, relative to younger adults. There was also indication that the pattern of within-category decline seen in younger undergraduates was not reproduced in the older sample: the older adults did not show a decline in performance for strong targets, and the increase in response time towards the end of each category was not as pronounced as for the younger participants. Thus, the disproportionate impact of ageing, as seen in the absence of within category decline for strong targets perhaps suggests that deficits in control mechanisms during initial retrieval reduce the need to suppress competitors on later trials, thus maintaining classification within categories.

2. Older adults vs. SA patients

The effects of three within-subjects factors were examined in a GLM: (1) *relatedness* (targets with a strong or weak association with the category), (2) *set* (comparison of task performance in the first half of each session compared with the second half of each session, to assess the possibility of general cognitive fatigue); and (3) *within-category* position (comparison of task performance in the first half compared with the second half of each category), plus *group* as a between-subjects factor. These predictors were entered in a fully-factorial model, including RT as a covariate. This study also modelled *category number* (i.e., performance for each of the five categories within each set) and *session number* (i.e., day 1 or day 2 of testing) without interaction terms, to capture these aspects of the design. Similar analysis was used for the RT data (see Table 3.3 for all *Wald* χ^2 and *p* values). Performance across the dependent measures is discussed separately for the three main factors of interest – (1) Relatedness, (2) Within-category performance, and (3) Set performance.

Table 3.3: Summary of significant results from the GLM analysis for SA patients and age-matched controls – looking at the effects of group, relatedness, set and within-category performance, for the key dependent measures- response sensitivity and response times.

Older adults vs. SA patients		
	<i>Response Sensitivity</i>	<i>Response Times</i>
Fixed effects:	Wald χ^2, <i>p</i>	Wald χ^2, <i>p</i>
Group	<i>3.19, p = .074</i>	<i>p > .1</i>
Relatedness	126.95, <i>p</i> < .001	410.63, <i>p</i> < .001
Set	<i>p > .1</i>	<i>p > .1</i>
Within-category	<i>p > .1</i>	<i>p > .1</i>
Interactions:		
Group x Relatedness	8.08, <i>p</i> = .004	<i>p > .1</i>
Group x Set	<i>3.42, p = .064</i>	<i>p > .1</i>
Group x Within-category	<i>p > .1</i>	<i>2.85, p = .092</i>
Set x Relatedness	<i>p > .1</i>	<i>3.20, p = .074</i>

Footnote: Table presents analyses employing (i) mixed effects modelling for response sensitivity (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest), and (ii) mixed effects modelling for response times (i.e., GLM preserving performance information for each category for each participant).

(1) Relatedness

The main effect of relatedness was significant across the dependent measures (see Table 3.3 for all *Wald χ^2* and *p* values). The response sensitivity model elicited a significant two-way interaction between *group* and *relatedness* (see Figure 3.5): sensitivity was lower for weak items in comparison to strong items across both groups but separate analyses split by group showed that relatedness had a larger effect on performance for the patients: *Wald χ^2 (1) = 101.43, p < .001*, than for the controls: *Wald χ^2 (1) = 34.64, p < .001*. The patients showed poorer performance, relative to controls, for weak associations.

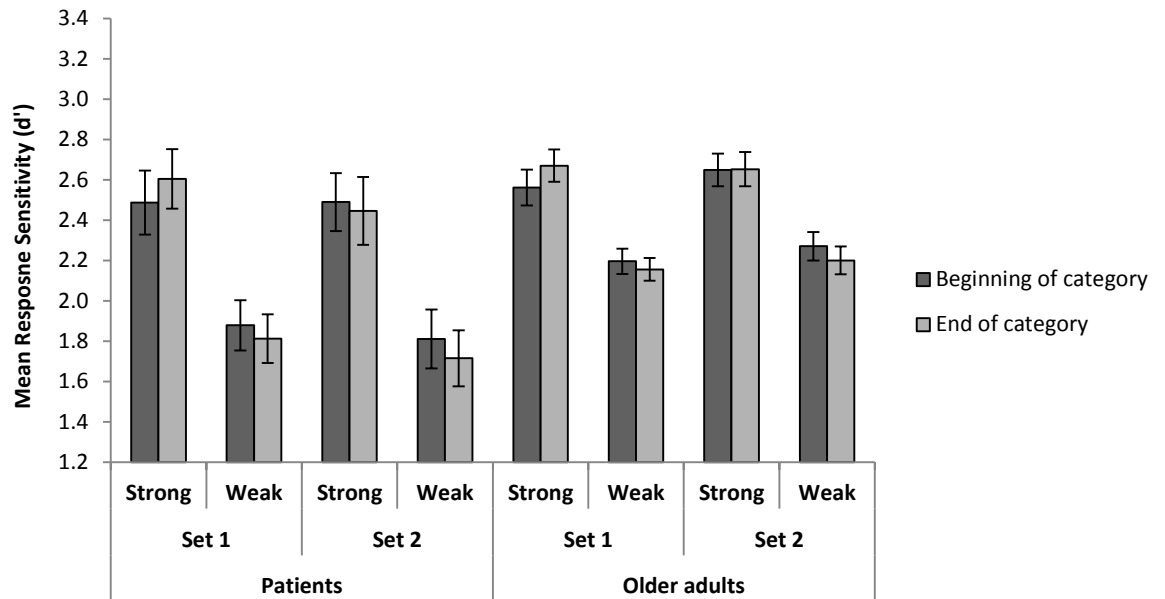


Figure 3.5: Mean response sensitivity (d') for the first and second half of each category (within-category performance), across the testing session (Set 1: first half of session, Set 2: second half of session), split by strong and weak targets for patients and controls. Error bars show *SE* of the mean.

(2) Within-category performance

Main effect of within-category performance was not significant across the dependent measures. There was however a significant interaction between *relatedness* and *within-category* performance in response sensitivity: there was a within-category decline in performance for the weak targets and a subtle improvement in performance for the strong items towards the end of each category (see Figure 3.5). This interaction was significant in both groups; Controls: $Wald \chi^2(1) = 18.98, p < .001$; Patients: $Wald \chi^2(1) = 8.718, p = .003$.

(3) Set performance

There was no significant main effect of set performance. The response sensitivity model revealed an interaction between *group* and *set* that was approaching significance ($p = .064$): patients showed a slight decline in performance from the first half of each session to the second half (see Figure 3.6), potentially reflecting fatigue, while controls showed a slight improvement in performance towards the second half of each session. However, the main effect of set in each group was not significant ($p > .1$).

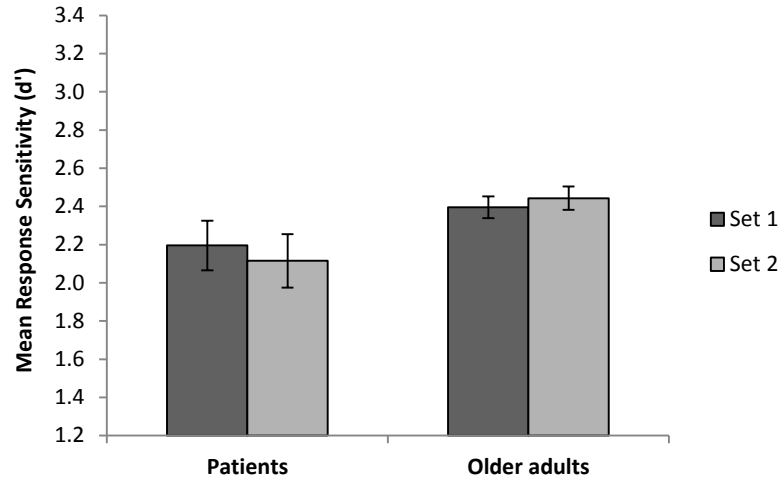


Figure 3.6: Mean response sensitivity (d') plotted using estimated means from the GLM, for the first half and second half of each session, for patients and controls. Error bars show SE of the mean.

There was also a trend-level interaction between *set* and *relatedness* ($p = .074$) in the RT model: there were comparatively faster response for strong items in the second half of the session, and slower responses for weak items (see Figure 3.7). This interaction was significant in the patient model (set by relatedness: $Wald \chi^2(1) = 4.62, p = .032$), but not for controls ($p > .1$).

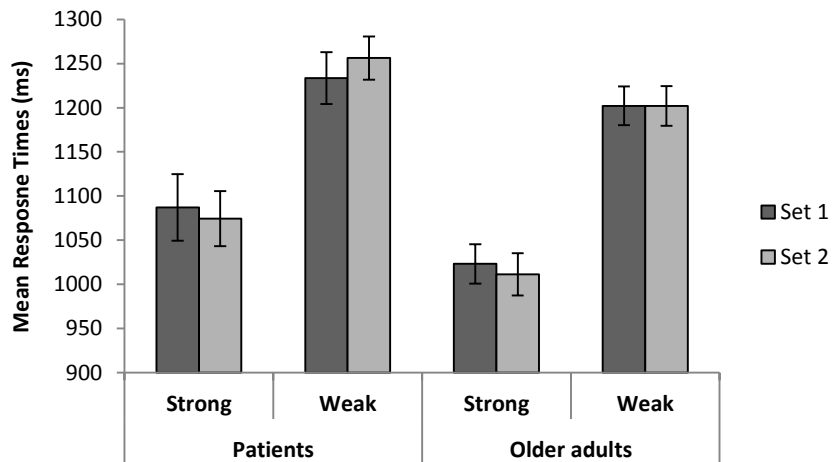


Figure 3.7: Mean response times (ms) plotted using estimated means from the GLM, for the first half and second half of each session, split by the strong and weak targets, for patients and controls. Error bars show SE of the mean.

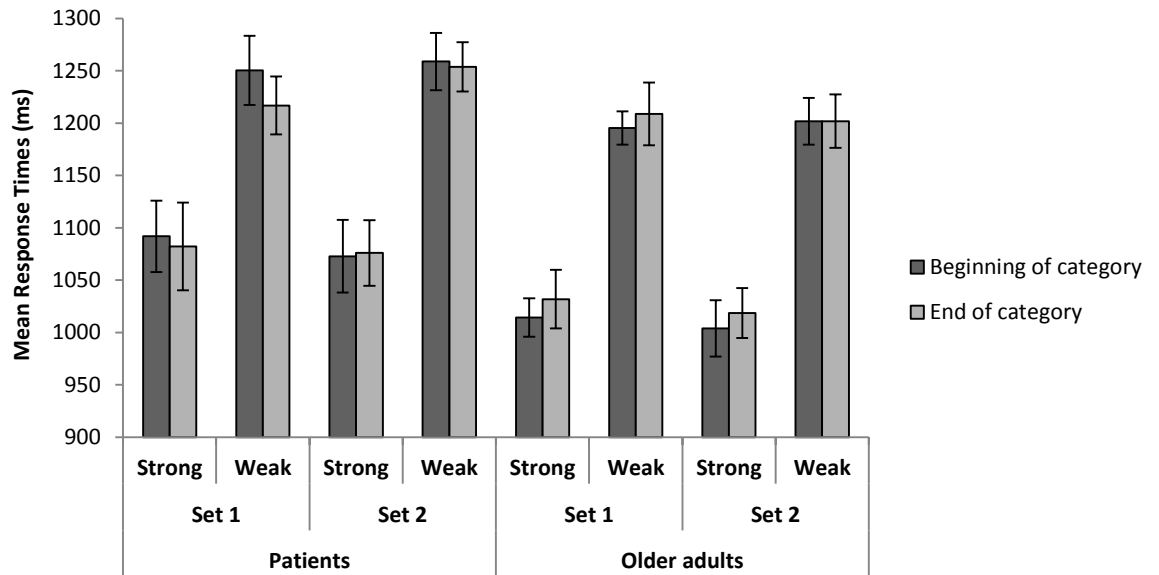


Figure 3.8: Mean response times (ms) for the first half and second half of each category (within-category performance), across the testing session (Set 1: first half of session, Set 2: second half of session), split by strong and weak targets for patients and controls. Error bars show *SE* of the mean.

3. Individual differences

This study further explores individual performance on the PSST paradigm in relation to subjective ratings of fatigue. Fatigue was assessed using the fatigue visual analogue scale (F-VAS), and correlations between fatigue ratings, PSST performance, refractory effects, and semantic/executive deficits were examined.

(1) Refractory task

Ten out of twelve patients performed a cyclical word-picture matching task in a separate testing session. As described earlier, SA patients are reported to show ‘refractory’ effects on cyclical matching tasks – i.e., declining comprehension when items are presented repeatedly (Gardner et al., 2012; Jefferies et al., 2007; Thompson et al., 2015). However, it is unclear whether ‘refractory’ effects are linked to the difficulty of sustaining a specific focus for semantic retrieval (e.g., whether patients who show within-category decline on the PSST will also show ‘refractory’ effects). It is also unclear whether this deterioration in comprehension over repeated trials is connected to cognitive fatigue more generally. Response efficiencies were computed for each cycle, and performance from cycle 1 to cycle 4 was compared to assess refractory effects (see Figure 3.9). Individual response times and accuracy are reported in Table 3.4.

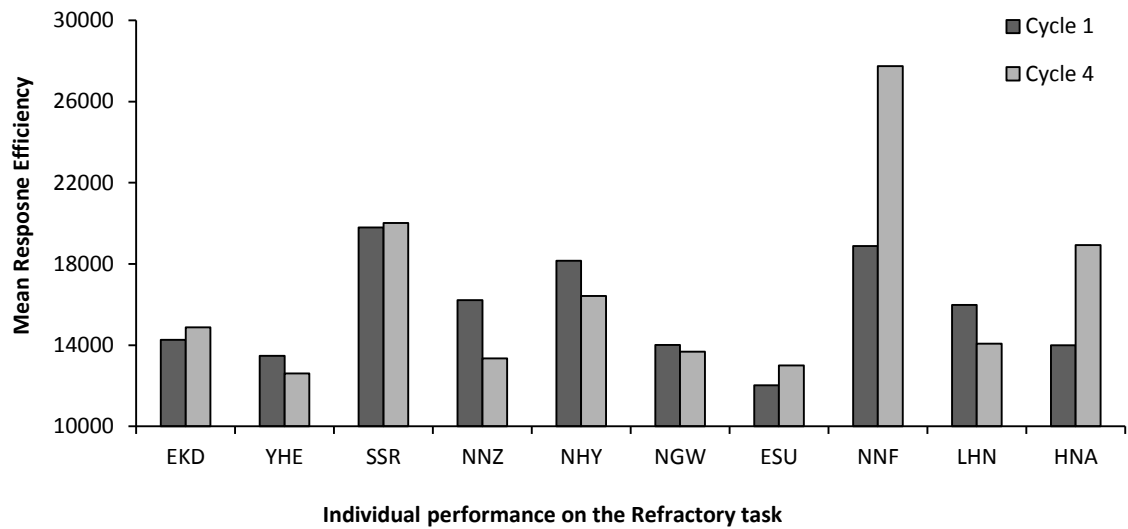


Figure 3.9: Mean response efficiency for the refractory task, for cycles 1 and 4, across all patients. Patients are arranged according to composite semantic severity scores. A higher efficiency score shows poorer performance.

Table 3.4: Refractory task performance on cycles 1 and 4, showing individual accuracies and response times, patients are arranged according to their composite semantic severity scores.

Patient	Accuracy (%)			RT (ms)		
	Cycle 1	Cycle 4	<i>p</i> -values (chi-square)	Cycle 1	Cycle 4	<i>p</i> -values (t-test)
EKD	98	98	.234	2783	2899	.472
YHE	98	98	.234	2621	2449	.527
SSR	78	80	.090	3070	3204	.684
NNZ	90	90	.791	2894	2364	.463
NHY	90	95	.446	3210	3099	.105
NGW	95	98	.282	2663	2666	.601
ESU	95	95	.406	2285	2470	.801
NNF	85	60	.002	3212	3329	.266
LHN	98	88	.529	3117	2462	.221
HNA	90	80	.386	2520	3028	.140

Footnote: Individual analysis based on refractory task performance: *p*-values reported using chi-square for accuracy and t-test based on trial-by-trial data for RT.

(2) PSST comparisons

It was assessed whether individual patient performance on PSST correlated with semantic/executive deficits, subjective fatigue ratings and performance on the refractory task. Effect sizes (percentage change) were computed in PSST performance based on five factors: *Relatedness* (overall difference in performance for strong compared to weak items), *Set effect for strong targets* (fatigue-related differences in performance for strong targets in the first half of the session compared to the second half), *Set effect for weak targets* (fatigue-related differences in performance for weak items in the first half of the session compared to the second half), *Within-category effect for strong targets* (differences in performance for strong items comparing the first half of each category to the second half), and *Within-category effect for weak targets* (differences in performance for weak targets comparing the first half of each category to the second half). Negative scores indicate percentage decreases for these measures (see Table 3.5 for individual scores). Correlations were examined between overall fatigue scores and a change in the subjective ratings of fatigue across the testing session, in addition to correlations with background testing and PSST performance (see Table 3.5 for individual fatigue ratings). All correlations are reported in Tables 3.6 and 3.7.

Table 3.5: Composite semantic and executive scores for all patients, along with their fatigue ratings, and PSST performance.

	EKD	ONY	YHE	SSR	RTJ	NNZ	NHY	NGW	ESU	NNF	LHN	HNA
Composite Semantic score	1.1	0.9	0.8	0.7	0.7	0.4	0.2	0.1	-0.4	-1.2	-1.2	-2.0
Composite Executive score	1.1	1.1	0.8	1.0	1.1	-0.4	-0.7	-0.7	-1.9	-0.2	-0.3	-0.9
PSST performance factors:												
1. Relatedness	-17.6	19.4	-16.9	24.7	-20.3	21.3	-22.5	-19.3	-19.0	-27.5	-16.9	-32.4
2. Set-strong	-5.6	-2.2	-0.4	-7.0	11.1	14.2	-6.8	-2.0	15.5	-0.5	23.6	-11.8
3. Set-weak	-6.0	0.8	-5.1	6.4	-2.8	1.6	0.1	11.1	11.7	3.4	28.4	13.0
4. Within-strong	-6.5	-5.0	6.3	-7.4	1.7	-3.1	9.9	-3.6	7.7	5.4	-7.9	4.5
5. Within-weak	-2.9	-5.5	5.8	-9.1	-2.8	-5.0	5.2	-1.5	6.9	-8.5	-6.3	0.9
Fatigue ratings (F-VAS):												
Beginning of session	4	0	4	0	3	5	2	6	0	2	1	1
Between session	7	0	6	0	3	5	5	6	0	3	1	2
End of session	8	0	9	0	5	6	6	5	0	4	1	4
Average score	6	0	6	0	4	5	4	5	0	3	1	2
Change in fatigue ratings	4	0	5	0	2	1	4	-1	0	2	0	3

Footnote: SA patients are arranged according to composite semantic severity scores; this is a single factor extracted from word-picture matching, Camel and cactus test pictures (CCTp) and words (CCTw), and synonym judgement. Executive composite scores are a single factor extracted from Trail making, Raven's Coloured Matrices and Brixton spatial rule attainment task.

Table 3.6: Correlations of PSST performance with semantic and executive performance, average fatigue ratings, changes in fatigue ratings across the session, and refractory task. All correlations within these factors are reported in Table 3.7.

	Composite semantic score	Composite executive score	Fatigue ratings	Change in fatigue ratings	Refractory task
	<i>r, p</i>	<i>r, p</i>	<i>r, p</i>	<i>r, p</i>	<i>r, p</i>
Relatedness	.600, .040	.220, <i>p</i> > .1	.240, <i>p</i> > .1	-.441, <i>p</i> > .1	.690, .030
Set-strong	-.110, <i>p</i> > .1	-.240, <i>p</i> > .1	-.190, <i>p</i> > .1	-.250, <i>p</i> > .1	.390, <i>p</i> > .1
Set-weak	-.710, .010	-.570, .060	-.540, .070	-.707, .010	.030, <i>p</i> > .1
Within-strong	-.270, <i>p</i> > .1	-.470, <i>p</i> > .1	.120, <i>p</i> > .1	.474, <i>p</i> > .1	-.320, <i>p</i> > .1
Within-weak	.020, <i>p</i> > .1	-.440, <i>p</i> > .1	.220, <i>p</i> > .1	.368, <i>p</i> > .1	.250, <i>p</i> > .1

Significant correlations

Of particular importance, there was *no* correlation between subjective ratings of fatigue and within-category decline, for either strong or weak items. Fatigue scores were also unrelated to task difficulty and severity of semantic/executive deficits. There were, however, a number of significant correlations:

- (i) The composite semantic score negatively correlated with the effect of set for weak items: $r = -.710, p = .010$: Patients with higher semantic scores showed a bigger decline in weak associations from the first half of the session to the second half, while those with lower scores actually showed an improvement in performance across the session (see Figure 3.10). Thus, there was no evidence that patients with poorer semantic cognition showed increased effects of fatigue, even within a task that required sustained attention to semantic processing.

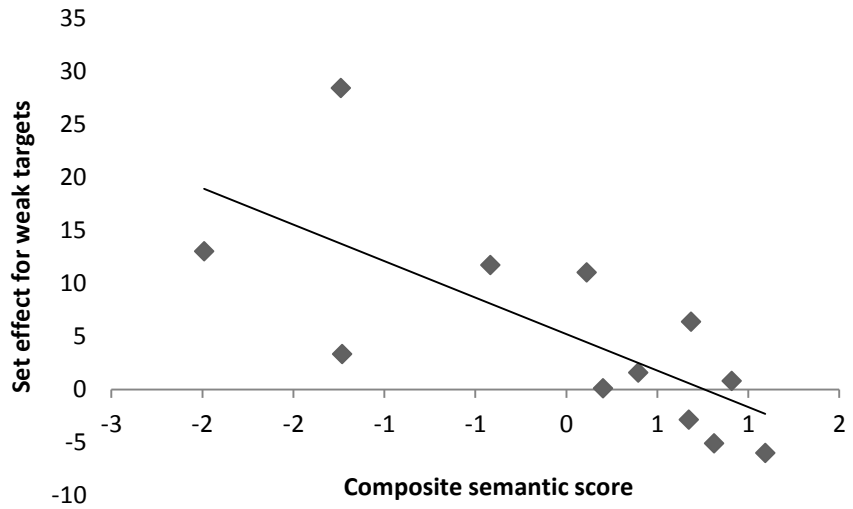


Figure 3.10: Correlation of composite semantic score and set effect for weak items: positive set score shows improvement at the task, while a negative score indicates a decline in performance.

- (ii) The composite semantic score positively correlated with relatedness: $r = .600$, $p = .040$: Patients with higher semantic scores showed a smaller effect of relatedness (see Figure 3.11).

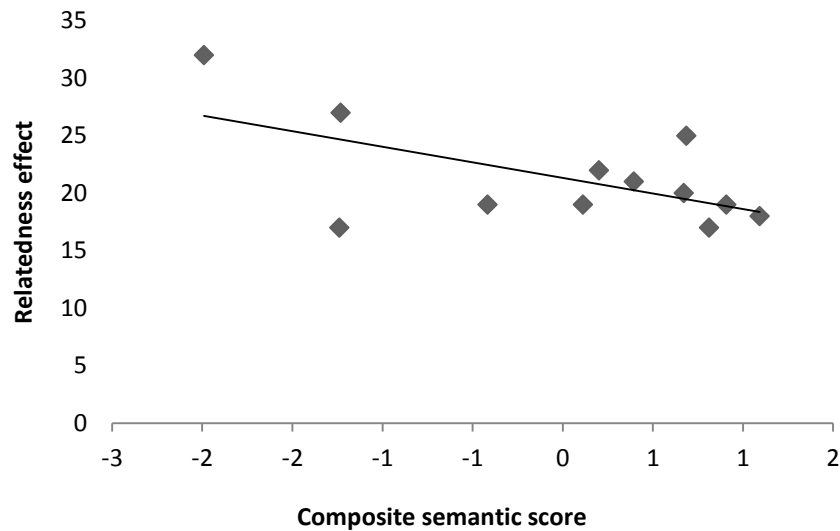


Figure 3.11: Correlation of composite semantic scores with relatedness: a higher relatedness score indicates a bigger difference in PSST performance for strong and weak targets.

- (iii) The change in fatigue ratings negatively correlated with the effect of set for weak items: $r = -.707$, $p = .010$. Patients who reported feeling more tired across the session showed a bigger decline in performance for the weaker associations from the first half of the session to the second half (see Figure 3.12). Thus, unlike composite measures of semantic or executive performance, subjective ratings of fatigue predicted declining performance on the task.

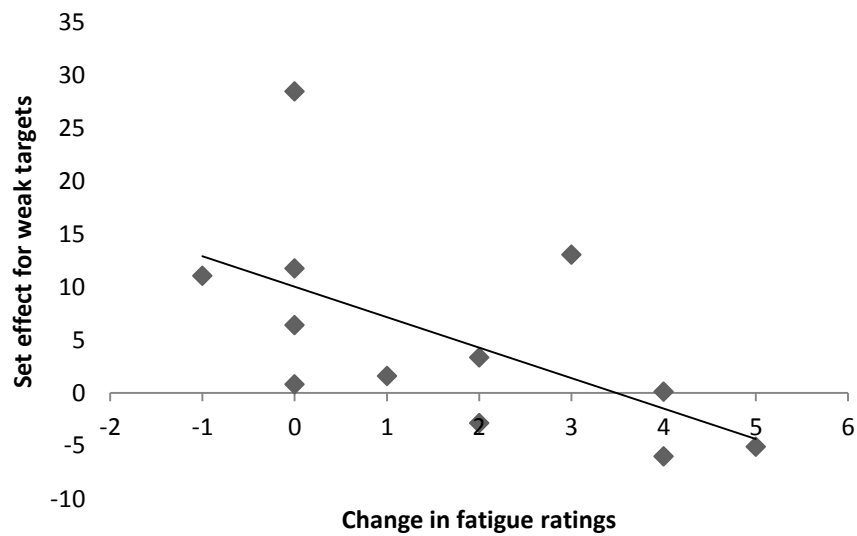


Figure 3.12: Correlation of change in fatigue ratings (a positive score indicates an increase in fatigue ratings across the session, and a negative score indicates a drop in the subjective ratings of fatigue across the session) with set effect for weak items (a positive set score shows improvement at the task, while a negative set score indicates a decline in performance).

- (iv) The magnitude of 'refractory' effects on the cyclical word-picture matching task correlated with relatedness: $r = .690$, $p = .030$. Patients who showed a bigger decline across cycles on the refractory task also showed the largest effects of relatedness (see Figure 3.13).

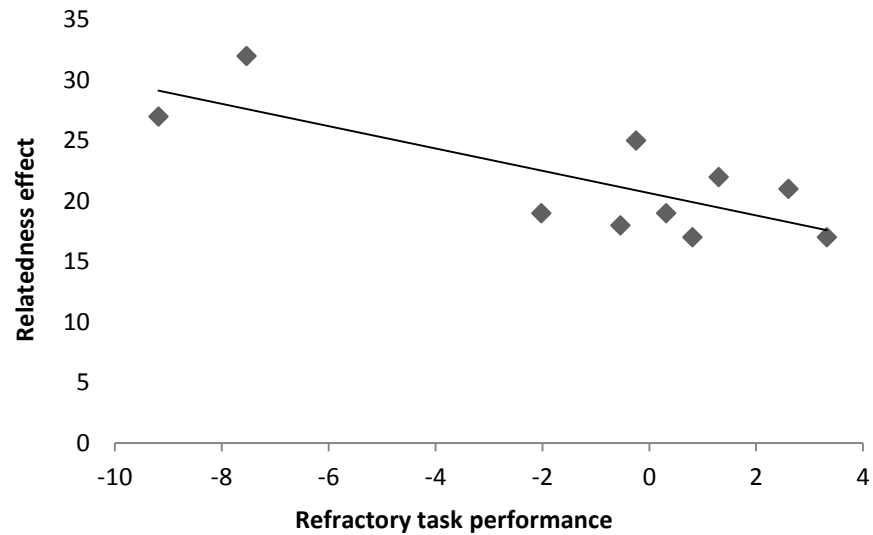


Figure 3.13: Correlation of performance on the refractory task with relatedness: a higher relatedness score indicates a bigger difference in PSST performance for strong and weak targets. A positive refractory score indicates an improvement, while a negative score indicates a decline on the refractory task.

Table 3.7: Correlations of performance within the PSST factors and within semantic and executive performance, average fatigue ratings, change in fatigue ratings across the session, and refractory task.

	Relatedness	Set-strong	Set-weak	Within-strong	Within-weak
	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>
Relatedness	1	.065, <i>p</i> > .1	-.147, <i>p</i> > .1	-.571, .053	-.474, <i>p</i> > .1
Set-strong	.065, <i>p</i> > .1	1	.433, <i>p</i> > .1	-.149, <i>p</i> > .1	-.059, <i>p</i> > .1
Set-weak	-.147, <i>p</i> > .1	.433, <i>p</i> > .1	1	-.234, <i>p</i> > .1	-.149, <i>p</i> > .1
Within-strong	-.571, .053	-.149, <i>p</i> > .1	-.234, <i>p</i> > .1	1	.724, .008
Within-weak	-.474, <i>p</i> > .1	-.059, <i>p</i> > .1	-.149, <i>p</i> > .1	.724, .008	1
	Composite semantic score	Composite executive score	Fatigue ratings	Change in fatigue ratings	Refractory task
	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>	<i>r</i> , <i>p</i>
Composite semantic score	1	.650, .022	.329, <i>p</i> > .1	.329, <i>p</i> > .1	.593, .071
Composite executive score	.650, .022	1	.187, <i>p</i> > .1	.187, <i>p</i> > .1	.187, <i>p</i> > .1
Fatigue ratings	.329, <i>p</i> > .1	.187, <i>p</i> > .1	1	.593, .042	.207, <i>p</i> > .1
Change in fatigue ratings	.108, <i>p</i> > .1	.231, <i>p</i> > .1	.593, .042	1	-.145, <i>p</i> > .1
Refractory task	.593, .071	.187, <i>p</i> > .1	.207, <i>p</i> > .1	.207, <i>p</i> > .1	1

Interim summary

The SA patients showed deficits of semantic and executive control and declining performance over time: however, these two impairments appeared to be largely independent. The semantic/executive impairment predicted greater deficits for weak associations on the PSST, and this effect of relatedness predicted the magnitude of one of the hallmarks of semantic access deficit – namely a decline in performance across cycles in a cyclical word-picture matching task. In contrast, the decline in performance over the whole of the testing session was related to subjective feeling of fatigue. The hypothesis that semantic or executive deficits might contribute to mental fatigue post-stroke was not supported.

Discussion

Semantic cognition is thought to involve semantic control processes that shape retrieval such that it is appropriate to the task or context. Ageing and semantic aphasia might influence control processes and the strength of conceptual representations in different ways. The data suggest that ageing has a disproportionate impact on the controlled retrieval of weak associations; furthermore, older adults did not show the decline in performance within categories for strong targets seen in younger participants. Patients with semantic aphasia showed even greater deficits in controlled retrieval (i.e., they maintained close-to-normal performance for strong associations, compared to older controls, but had additional difficulties identifying weakly-associated targets). SA patients resembled older adults in the effects of within-category decline for strong associations (i.e., there was little evidence of declining comprehension over successive targets within a category, in contrast to younger adults). This study also investigated the relationships between cognitive impairment, the capacity to sustain performance over time, and subjective feelings of fatigue, which are poorly characterised by past studies (for a review, see Lagogianni, Thomas, & Lincoln, 2016; Lerdal et al., 2009; Staub & Bogousslavsky, 2001). Some individuals in the stroke group showed a pattern of declining comprehension over the session, which correlated with subjective feelings of fatigue. While these fatigue effects clearly had consequences for semantic cognition, they were not predicted by indicators of semantic control deficits, such as the magnitude of the relatedness effect or refractory impairment in word-picture matching. This suggests that semantic control deficits and post-stroke cognitive fatigue are largely independent.

A reduced capacity to identify weak but not strong associations was found across the three groups of participants; with the poorest performance in SA and best performance in

younger participants. This difficulty with weakly-associated targets resembled the effect of the secondary task in Experiment 5, Chapter 2. Understanding the relationship between a probe category and a weakly-associated item is thought to require greater semantic control than identifying semantic links for strongly-associated items, since dominant but irrelevant features and associations have to be suppressed in order to allow the required weakly-instantiated knowledge to come to the fore (Noonan et al., 2009; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2010). The preserved performance for strong items in both older adults and SA patients is consistent with the hypothesis that knowledge itself is relatively unaffected by ageing and by damage to brain regions supporting semantic control; changes in semantic cognition in these groups might instead follow from difficulty constraining retrieval in a flexible fashion to suit the task requirements. There is already strong evidence for this proposal in patients with semantic aphasia (Corbett, Jefferies, & Ralph, 2011; Noonan et al., 2010), and this is consistent with their damage to left inferior frontal gyrus and/or posterior middle temporal gyrus, brain regions thought to be critical for semantic control (Badre & Wagner, 2002, 2007; Fiez, 1997; Jefferies & Lambon Ralph, 2006; Miller & Cohen, 2001; Noonan, Jefferies, Visser, & Ralph, 2013). In addition, neither older adults nor SA patients showed the decline in the detection of strong targets across successive trials within categories that characterised the performance of younger participants in Chapter 2. The fact that patients with well-documented deficits of semantic control, and associated impairments in the retrieval of weak associations, showed a reduced effect of within-category decline suggests that this pattern might reflect the suppression of non-target information to facilitate retrieval on earlier trials. These inhibitory weight changes could then affect later performance in healthy young participants, similar to the cumulative picture naming paradigm (Oppenheim, Dell, & Schwartz, 2010), while in patients with SA, the suppression of distractors on earlier trials would be attenuated and therefore within-category decline in performance would not occur. While our interpretation remains speculative, it might be that older healthy adults show attenuation of within-category decline for a similar reason. The findings from patients with SA are apparently inconsistent with the view that within category decline in categorisation occurs because of increasing levels of competition from previously-activated targets, because these patients should have greater difficulty resolving this competition, which would be expected to produce an exaggerated pattern of within-category decline. The findings, taken together, are therefore consistent with the view that patients with SA and to some extent older adults did not deal with the demands of initial retrieval by suppressing competitors, which subsequently made them less vulnerable to within-category decline.

This study also examined the relationship between declining categorisation on the PSST, semantic and/or executive impairments, and ‘refractory’ effects in cyclical matching tasks. It was found that semantic/executive impairment predicted greater deficits for *weak* associations on the PSST, and this effect of relatedness predicted the magnitude of ‘refractory’ effects. However, in contrast to performance on cyclical tasks, where SA patients are reported to show declining comprehension when items are presented repeatedly (Gardner et al., 2012; Jefferies et al., 2007; Thompson et al., 2015), these patients did not show the decline in categorisation performance within categories in the PSST, unlike the healthy younger volunteers in Chapter 2. One possibility is that these patterns of declining comprehension may reflect different mechanisms – for example, in the cyclical paradigm, there is the potential for on-going activation in a very simple task and so the structure of the task is designed to maximise competition. In a continuous paradigm, such as the PSST, targets are distributed amongst many distractors and so the structure of the paradigm is set up to detect slightly longer-term effects, and it is more likely that there will be retrieval-induced declines in performance, as seen in the previous chapter.

This distinction between these paradigms, however, enabled further examination of the underlying mechanisms contributing to within-category decline in the PSST. By one account, if categorisation on the PSST becomes harder as more and more related conceptual representations are primed by their previous presentation, this may give rise to increasing competition. Given that SA patients have difficulties resolving competition, the effects of within-category decline should be exaggerated in this group – in line with the increased difficulty in cyclical word-picture matching paradigms that SA cases also often show. In contrast, if within-category declines reflect a build-up of inhibition as a side-effect of controlling competition at the point of retrieval on earlier trials (i.e., retrieval-induced forgetting), this effect would be reduced or extinguished in the SA group. The findings support the latter view – i.e., retrieval-induced forgetting (e.g., Anderson, Bjork, Bjork, & Jordan, 2000), but in the domain of semantic memory, as it might be that the application of control to inhibit competitors in early trials within each category gives rise to this pattern of retrieval-dependent declines in categorisation. Therefore, semantic control can have differential effects on continuous retrieval, and evidence from both patients and older adults suggests that the capacity to employ control in a flexible way might be critical in overcoming the effect of retrieval-induced forgetting on later trials.

While the findings are consistent with a deficit of semantic control in SA, they also speak against a simple hypothesis concerning the relationship between the deregulation of semantic retrieval and mental fatigue post-stroke. It is plausible to assume that for individuals with greater

semantic and/or executive impairment, cognitive tasks are more tiring and this gives rise to mental fatigue. However, there was no evidence that more severely impaired cases showed greater decline in performance across the session. Even though refractory deficits involve declining comprehension over time (with release from this effect when the set of items is changed); there was no discernible correlation with fatigue in the current study – either with the fall in performance over blocks across the session, or with subjective feelings of mental tiredness. This suggests that semantic control deficits and fatigue are broadly independent. Moreover, fatigue ratings correlated with the decline in comprehension for *weak* items over the course of the task, so patients appear to have some insight into their declining comprehension. These findings further elucidate the nature of the semantic impairment in SA and establish that while both mental fatigue and deficits of controlled semantic retrieval are common consequences of stroke, they are not likely to have a common cause.

Chapter 4

Electrical enhancement of the left inferior frontal gyrus modulates semantic and executive control processes within a paced comprehension task

Acknowledgements: This study was conducted in collaboration with a 3rd year undergraduate project, where students helped with collecting images, ratings, and with the data collection:

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Abstract

Semantic cognition requires not only a semantic store, but also a system for retrieving and selecting stored information as goals dictate. Left inferior frontal gyrus (LIFG) has been particularly associated with controlled access to semantic knowledge. In the present study, transcranial direct current stimulation (tDCS) was applied to LIFG to modulate performance on an auditory paced serial semantic task, which required sustained categorisation consistent with current goals. Previous research has shown that semantic categorisation deteriorates over the course of each category in this task, particularly for strongly-associated targets, this study tested the hypothesis that this effect would be reduced by the application of anodal tDCS. Strength of association was manipulated between the category and target, as well as the presence or absence of distracting visual information. There were positive effects of stimulation, particularly in response times. Benefits of stimulation were observed at different time points during the task: (i) Categorisation of weak items was enhanced at the beginning of categories, when it was hardest to retrieve less common associations. (ii) The classification of strong items was enhanced by tDCS towards the end of the categories, as stimulation ameliorated the decline in continuous classification. (iii) tDCS also augmented learning effects in categorisation, particularly when congruent visual images were presented alongside the spoken words. Together these results constrain accounts of the role of LIFG in semantic retrieval and build on literature suggesting that stimulation of this region can facilitate conceptual retrieval.

Introduction

Semantic cognition involves processes and representations that underlie our ability to comprehend the environment; it is thought to require a combination of semantic representations and control processes to apply knowledge to a specific context or direct retrieval towards a goal (Jefferies & Lambon Ralph, 2006). Functional neuroimaging and neuropsychological studies have both suggested that semantic representation and control processes are supported by distinct areas in the human brain (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Hoffman, Binney, & Lambon Ralph, 2015; Jackson, Hoffman, Pobric, & Lambon Ralph, 2015; Jefferies, 2013; Jefferies & Lambon Ralph, 2006). Ventral anterior temporal regions are thought to form a central semantic store (Patterson, Rogers & Nestor, 2007), while LIFG has been frequently associated with semantic control processes, such as the controlled retrieval or selection of information (Badre & Wagner, 2002, 2007; Fiez, 1997; Jefferies & Lambon Ralph, 2006; Miller & Cohen, 2001; Noonan, Jefferies, Visser, & Ralph, 2013).

In neuroimaging studies, LIFG activity has been observed during tasks requiring controlled access to semantic knowledge when the link between the probe and target is weak, and circumstances where there is competition and high selection demands (Badre et al., 2005; Nagel, Schumacher, Goebel, & D'Esposito, 2008; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Maril, Bjork, & Schacter, 2001). LIFG responds strongly to lexical selection (in tasks involving the resolution of lexical ambiguity, or word generation), and the need to select from competing alternatives in cognitive control paradigms (such as Stroop or working memory tasks; Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1997; for reviews see Novick, Trueswell, & Thompson-Schill, 2010). Similar results were presented in a study by Moss et al. (2005) using a picture naming task including competitor priming. However, other research has revealed a role for LIFG in tasks with low selection demands yet requiring effortful retrieval, such as generating verbs from concrete nouns when there is only one associated action (Martin & Cheng, 2006). This suggests that LIFG plays a role in multiple aspects of semantic control – both selection from competing alternatives and controlled retrieval in the absence of selection, when target representations are only weakly facilitated by the context (Badre et al., 2005; Raichle et al., 1994; Wise et al., 1991).

Converging evidence from neuropsychology and brain stimulation has also implicated LIFG in controlled aspects of semantic cognition (Krieger-Redwood & Jefferies, 2014; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). For example, Hoffman et al. (2010) showed reduced comprehension of abstract words in both patients with LIFG damage and healthy

participants following inhibitory TMS to LIFG, plus a strong sensitivity to cues that reduced the requirement for controlled retrieval in both of these samples. Casual inferences can also be drawn from the effects of transcranial direct current stimulation (tDCS): depending on the polarity of the current used, brain excitability can either be increased by anodal tDCS or decreased by cathodal stimulation (Liebetanz, Nitsche, Tergau, & Paulus, 2002). Hence, tDCS does not necessarily 'stimulate' neurons but modifies the ongoing activity within regions (Nitsche & Paulus, 2000). These effects are maximal under the stimulating electrode and within functionally-coupled regions (see Joyal & Fecteau, 2016 for reviews; Miniussi, Harris, & Ruzzoli, 2013). tDCS is therefore a potentially suitable method for influencing the extent to which the retrieval of one item disrupts the availability of a related concept, since these effects may reflect a dynamic balance between excitatory and inhibitory connections (cf. Barron et al., 2016).

In the domain of language, tDCS studies have shown that anodal stimulation of LIFG facilitates grammar learning (de Vries, Barth, & Maiworm, 2010), picture naming (Fertonani, Rosini, Cotelli, Rossini, & Miniussi, 2010; Henseler, Mädebach, Kotz, & Jescheniak, 2013; Holland et al., 2011) and verbal fluency (Cattaneo, Pisoni, & Papagno, 2011; Iyer et al., 2005; Penolazzi, Pastore, & Mondini, 2013; but see Vannorsdall et al., 2016). Anodal tDCS to this region promotes recovery of picture naming in aphasic participants (see Monti et al., 2013 for reviews; Fiori et al., 2011; Fridriksson, Richardson, Baker, & Rorden, 2011; Marangolo et al., 2011). While these studies all involved speech production, anodal tDCS to the left inferior frontal cortex facilitated contextual selection and controlled semantic retrieval in a semantic judgement task with lexical ambiguous words (see Ihara, Takanori, & Soshi, 2014), and improved the selection of low-dimensional items or items weakly associated with a category (Lupyan, Mirman, Hamilton, & Thompson-Schill, 2012). Anodal stimulation of the left lateral prefrontal cortex facilitated idiom comprehension (see Sela, Ivry, & Lavidor, 2012) and complex verbal problem solving on the remote associates task (RAT), which requires participants to suppress dominant associations (Cerruti & Schlaug, 2009; see also Metuki, Sela, & Lavidor, 2012). Anodal stimulation of LIFG also facilitated relatedness judgements for gestures accompanying language (Cohen-Maximov, Avirame, Flöel, & Lavidor, 2015; Schülke & Straube, 2016), suggesting that these effects are not restricted to verbal stimuli.

There are also studies showing that tDCS to left PFC can modulate semantic interference in picture naming: for example, after stimulation, participants showed an attenuated effect of repeatedly accessing related sets of semantic pictures in a blocked paradigm (Meinzer, Yetim, McMahon, & de Zubicaray, 2016; Pisoni, Papagno, & Cattaneo, 2012; Wirth et al., 2011). Meinzer

et al. (2012) showed that anodal stimulation of LIFG improved lexical retrieval and reduced accompanying activation of LIFG, and also increased the connectivity of this region with other brain areas underlying the language network. This could possibly reflect strengthening of top-down control processes following LIFG stimulation.

The present study investigated if anodal tDCS over LIFG would modulate performance on a continuous categorisation paradigm in healthy young participants. The PSST paradigm from Chapters 2 and 3 was used to examine the effects of stimulation on multiple factors thought to influence semantic control demands. (i) Effects of stimulation were compared in the first half and second half of each category, since controlled retrieval demands may be initially high (in the absence of priming of semantically-relevant features) but continuous categorisation also deteriorates with successive targets (see Chapter 2), potentially reflecting either activation of competing information following the retrieval of previous targets (Campanella & Shallice, 2011), or the suppression of relevant information that may follow from the retrieval of earlier targets (i.e., a by-product of the control of competition at the time that previous targets were retrieved; Oppenheim, Dell, & Schwartz, 2010). (ii) The strength of association was also manipulated between the probe category and the target, since controlled retrieval demands are higher for weakly-associated targets, and this effect should be particularly clear towards the beginning of each category in the absence of priming. Moreover, the decline in performance during continuous categorisation within a specific category interacts with strength of association (see Chapter 2): successive weight changes elicited during the previous retrieval of related items may be more marked when targets are strongly associated with the probe and/or they may experience more competition from previously-retrieved items. Thus, it might be envisaged that tDCS could boost the retrieval of weak associations initially, but later have a more protective effect on the retrieval of strong associations by preventing decline during continuous categorisation. (iii) The presence of distracting visual information during auditory semantic categorisation was also manipulated. Auditory targets were presented concurrently with relevant or irrelevant images to determine whether tDCS to LIFG would boost selective retrieval driven by the auditory input and ameliorate the effects of visual distractors. Based on current knowledge, this is the first study that has examined the effects of tDCS on continuous semantic retrieval: this is an important step with potential implications for enhancing performance and for rehabilitation. This design also permitted a comparison of the effects of LIFG stimulation on factors tapping selection/inhibition (presence of distracting visual information) and controlled retrieval (initial performance for weak vs. strong associations).

Methods

Participants

A total of 32 undergraduate students participated in this experiment (20 females and 12 males), in return for course credit or a payment of £20. Mean age of the students was 24 years (SD = 2.62; range of 18-29). All participants were native English speakers, right-handed, with normal to corrected-to normal vision and hearing and with no known neurological or psychiatric conditions including epilepsy. For safety purposes, potential participants were excluded, if they were using medication that might affect the central nervous system, those with neurological and psychiatric conditions including a history of seizure, previous surgery or metal in the head or upper body, pregnancy, and the use of alcohol, drugs or excessive caffeine.

Task and Design

The 'Paced Serial Semantic Task' or PSST required rapid semantic association judgements that linked spoken words to a functional category. Participants were given a category, such as PICNIC or HOSPITAL and were asked to classify spoken words in terms of whether they were associated with the target categories.

Materials

Forty-eight different category labels were used, twenty-four presented in each session, twelve categories at the beginning of session (baseline block) and twelve at the end (stimulation block). There were 40 items in each category (such as CAFE), 20 items were related to the category, including 10 targets that were strongly related to the category label, such as "*coffee*"; and 10 that were distantly related, such as "*apron*", while the remaining 20 items were unrelated to the category (e.g. "*nurse*") – these were recycled items from other categories (see Appendix C and F for a complete list of items used).

Of the twelve categories presented in each block, six categories were presented in an eyes closed condition (only auditory items, participants were also asked to wear an eye mask in this condition) and the remaining six were presented in an eyes open condition (auditory targets presented along with visual distractors). These images were colour photographs on a white background; either congruent or incongruent to the auditory target (see Figure 4.1). As participants responded on every trial, items were presented at a speed of 1.5 seconds, in the eyes open condition participants were still to only respond to the auditory stimuli that were related or unrelated to the category, regardless of the picture that was presented. Target words were

selected using the Edinburgh Associative Thesaurus (EAT; Kiss, Armstrong, & Milroy, 1973), and images were collected for these words; this was supplemented by a pilot study in which ratings were collected for the relatedness of each word to the category label. Participants (N = 15) used a 7-point Likert scale to judge relatedness, and items were categorised as strongly related (> 5.5), weakly related (2.2 - 5.5) or unrelated (< 2.2).

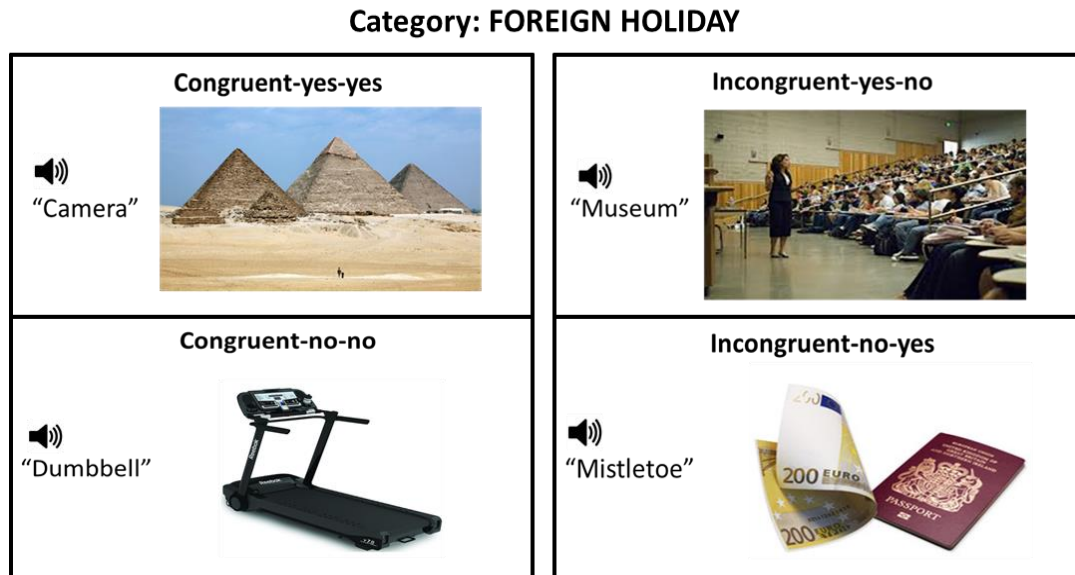


Figure 4.1: The four congruency conditions presented in the eyes open block, participants responded to the auditory items and were asked to ignore the pictures in a – ‘congruent-yes-yes’ condition: both word and picture were related to the category; ‘incongruent-yes-no’: only word related to the category; ‘congruent-no-no’: both word and picture unrelated to the category; and ‘incongruent-no-yes’: only picture related to the category.

Stimulation parameters

A constant direct current (2 mA) was administered by a battery-driven stimulator (DC-Stimulator, NeuroConn, Ilmenau, Germany). The stimulating electrode was inserted in a saline-soaked synthetic sponge (7 cm × 5 cm, 35 cm²) and centred over the LIFG (i.e., site F7, position delineated according to the international 10–20 EEG system). The reference electrode was placed on the right shoulder of the participant. In both the anodal and sham conditions there was a ramp up/ramp down period of 30 seconds at the start and end, eliciting a tingling sensation on the scalp that faded over seconds. The current was turned off after 30 seconds (sham) or continued for a total of 10 minutes during anodal tDCS. Participants filled out a ‘sensation form’ (Fertonani et al., 2010) at the end of each session which evaluated the sensations felt during stimulation (e.g., pain, burning, itchiness, etc.) on a five-point scale (“1” = no sensations, “5” = strong sensations).

Procedure

The experiment was run using E-Prime 2.0 (Psychology Software Tools, Sharpsburg, PA). Testing was completed across two days, separated by at least 24 hours. All participants completed two one hour sessions. Each session began with a practice block, which consisted of two categories presented in an eyes closed condition and two categories in an eyes open condition, this was followed by the two experimental blocks: baseline block (without stimulation) and stimulation block (sham/anodal tDCS). During both sessions participants first completed the baseline block followed by stimulation and the delivery of stimulation started simultaneously with the second block (the order of sham or anodal stimulation was alternated across participants). Both baseline and stimulation included equivalent numbers of eyes open and eyes closed trials. Hence, the order of sham and anodal sessions, order of categories, and the order of trials was fully counterbalanced across participants.

Results

Statistical analysis

In line with the previous experiments, generalised linear models (GLMs) using generalised estimating equations (GEE) were used for all analyses. Performance was assessed in the block following stimulation (or sham stimulation) and baseline performance was entered as a covariate. Two parallel analyses were then used: (i) response sensitivity (d') was computed, which accounts for response bias (the general tendency to respond *yes* or *no*; Stanislaw & Todorov, 1999). Aggregate d' scores were used for each participant per category, and average RT was entered as a covariate. (ii) Separate GLMs were further used on the RT data (average performance per trial) using baseline RT and response sensitivity as a covariate. This allowed for the assessment of changes in response sensitivity taking RT into account and changes in RT performance taking accuracy into account, while also controlling for the average performance in the baseline session. All factors included in the GLMs are listed separately under each model below.

In order to prevent overestimation or over-fitting of the models (as this study had more experimental manipulations and potentially high-order interactions compared with previous chapters), the GLM analysis was started with an unconditional (empty) model, which contained no predictors but allowed the intercept of the dependent variables (i.e., response sensitivity/response times) to vary by the repeated-measure variables (i.e., participant number). The Quasi-likelihood under Independence Model Criterion (QIC) was used, which is an adaptation of the AIC goodness-of-fit measure for repeated-measures designs (with smaller values indicating

better fit; Cui & Qian, 2007). QIC from the empty model allowed comparison with later models; thus QIC enabled the selection of the best subset of predictors/interactions for the final model.

Results are presented based on the following two models: 1. *Eyes closed vs. eyes open* – this included data from the full set of trials. 2. *Eyes open with congruent vs. incongruent visual stimuli* – which further assessed performance in the eyes open condition by splitting performance based on pictures related (congruent) or unrelated (incongruent) to auditory items.

1. Eyes closed vs. eyes open

The effects of the following fixed within-subjects factors was examined in a repeated-measures GLM: (a) *closed-open* (performance on trials with eyes closed compared with eyes open), (b) *sham-anodal* (performance split by trials with sham stimulation compared with anodal stimulation), (c) *relatedness* (strong vs. weak items), and (d) *within-category* position (comparison of task performance in the first half compared with the second half of each category). The *day of testing* (i.e., day 1 or 2 of testing) was also modelled without the interaction terms, to capture all aspects of the design. Separate models were run on: (1) *response sensitivity* and (2) *response times*, including baseline performance and average RT/sensitivity as a covariate respectively. Following the empty model, a fully factorial model was entered in the GLM. The next model included effects that were significant in the previous model. This way, the analysis concluded with a model which provided the best fit, measured using the QIC, reported in Table 4.1. All significant *Wald* χ^2 and *p* values from the final model have been reported in Table 4.2. Paired contrasts were also available within the GLM, based on the estimated marginal means of the dependent variables (i.e., response sensitivity and response times), for all-level combinations of the factors of interest. Pairwise contrasts for all *sham-anodal* comparisons presented in each figure have been reported in Table 4.4 to aid interpretation of the interaction effects.

Table 4.1: Results from the GLM for the Quasi-likelihood under Independence Model Criterion (QIC), for the unconditional or empty model, full-factorial model and the last model, shown individually for the Eyes closed vs. open model and the Congruent vs. incongruent model.

		1. Eyes closed vs. open		
		<i>Empty model</i>	<i>Full-factorial model</i>	<i>Final model</i>
QIC	Response Sensitivity	335.38	308.28	288.91
	Response Times	2871170.07	2632472.91	2632472.91
		2. Eyes open: Congruent vs. Incongruent		
		<i>Empty model</i>	<i>Fully-factorial model</i>	<i>Final model</i>
QIC	Response Sensitivity	598.23	434.15	416.75
	Response Times	4686307.01	3883182.00	3883182.00

Table 4.2: Summary of significant results from the GLM analysis for the eyes closed vs. open model – looking at the effects of eyes (closed vs. open), stimulation type (sham vs. anodal), relatedness (strong vs. weak targets) and within-category performance, for the key dependent measures – response sensitivity and response times.

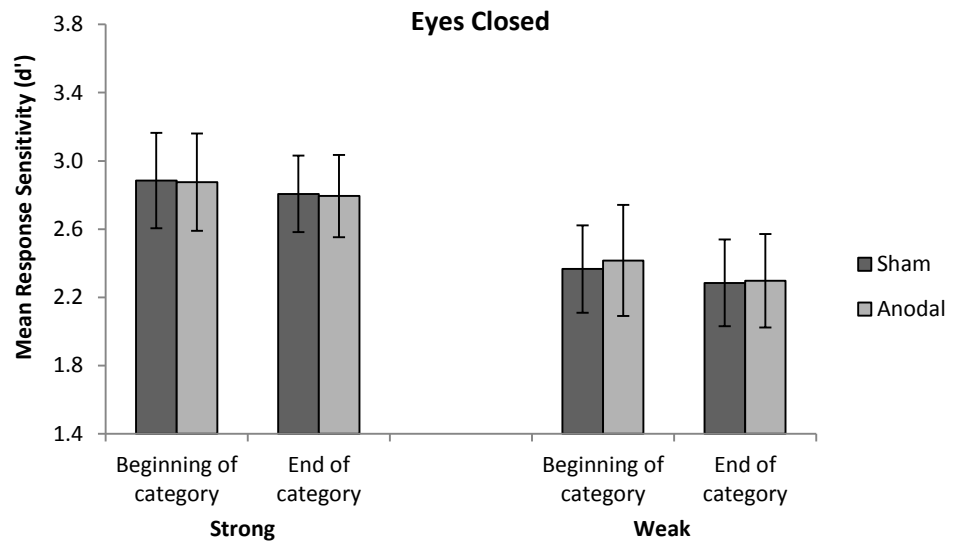
Eyes closed vs. open		
	<i>Response Sensitivity</i>	<i>Response Times</i>
Fixed effects:	Wald χ^2, <i>p</i>	Wald χ^2, <i>p</i>
Closed-Open	<i>p</i> > .1	<i>p</i> > .1
Sham-Anodal	<i>p</i> > .1	<i>p</i> > .1
Relatedness	116.41, < .001	262.80, < .001
Within-category	<i>p</i> > .1	3.896, .048
Significant interactions:		
Closed-Open x Relatedness	33.90, <i>p</i> < .001	4.41, .036
Relatedness x Within-category	-	12.99, < .001
Closed-Open x Sham-Anodal x Relatedness x Within-category	-	16.88, .051

Footnote: Table presents two analyses employing (i) mixed effects modelling for response sensitivity (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) mixed effects modelling for response times (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed *d'* per category to be included as a covariate of no interest).

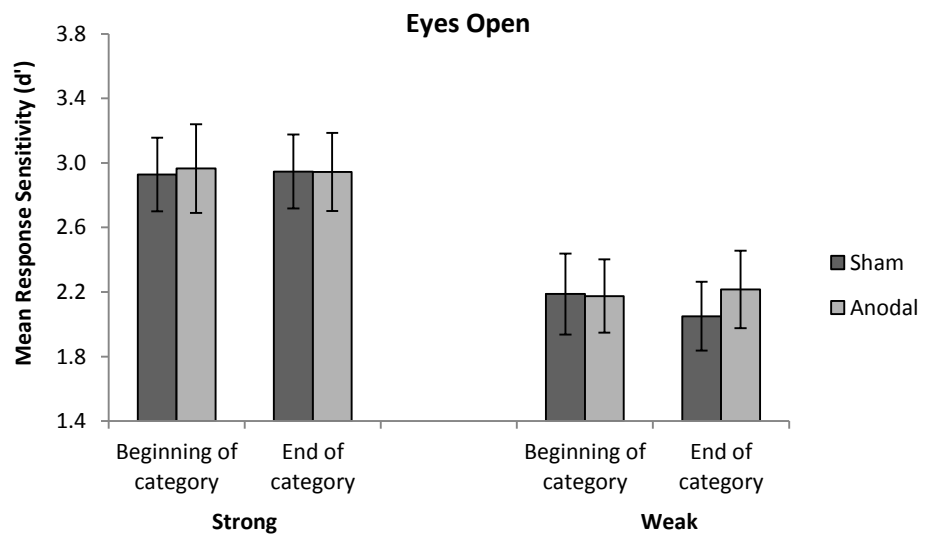
(1) Response Sensitivity

There were no significant effects of stimulation, the response sensitivity model revealed only a significant main effect of relatedness and a significant interaction between eyes (closed vs. open) and relatedness (see Table 4.2 for all *Wald* χ^2 and *p* values): Participants' sensitivity in categorising strongly-related targets items was the same across both eyes closed and open

conditions, however, the categorisation of weak items was poorer in the eyes open condition. Consequently, the effect of strength of association was greater with eyes open than closed (see Figure 4.2).



Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals



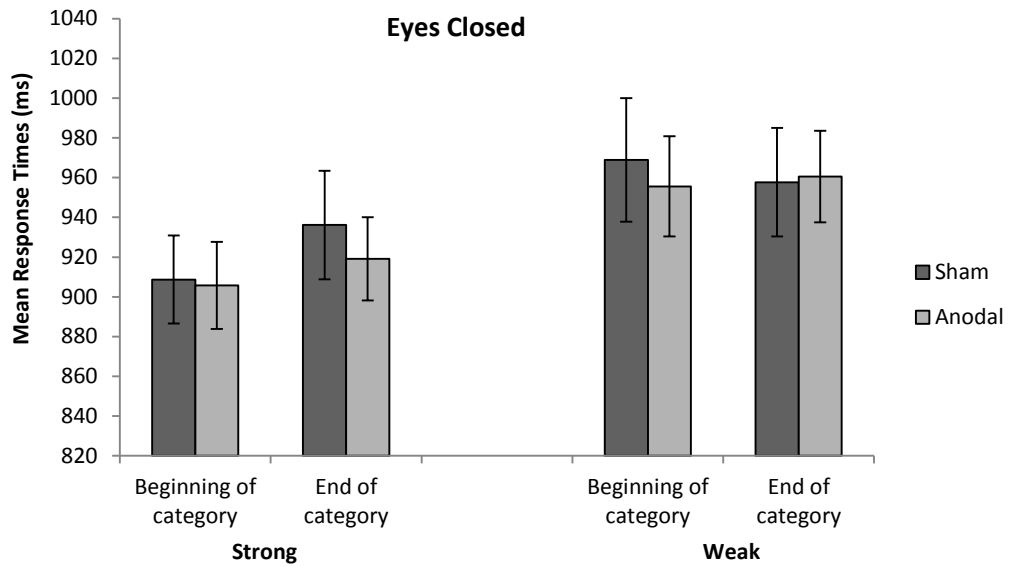
Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals

Figure 4.2: Mean response sensitivity (d') for the strong and weak targets in the first half and second half of each category (within-category fatigue), comparing performance in the sham and anodal conditions, and shown individually for the eyes closed and eyes open conditions.

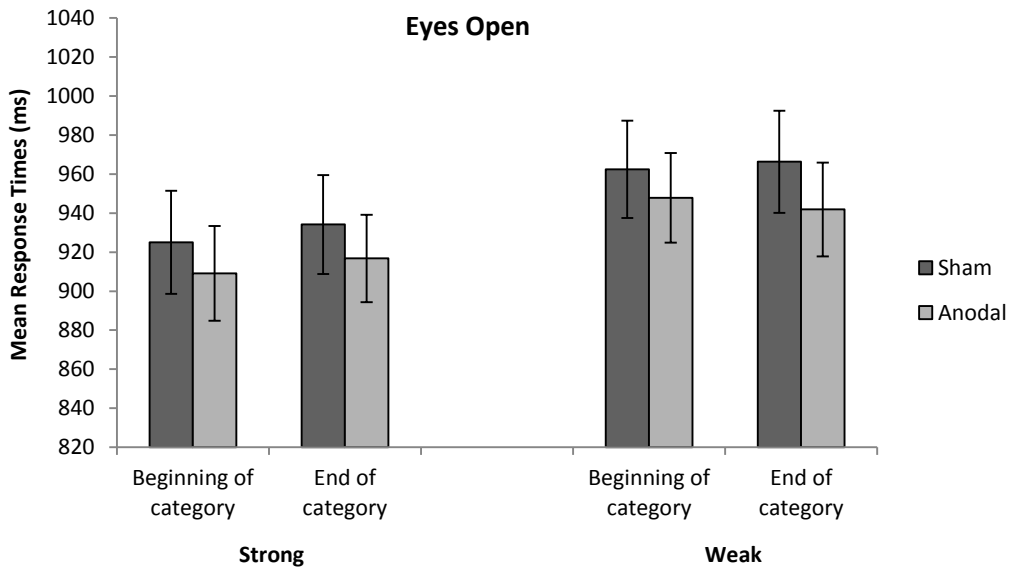
(2) Response Times

There were significant main effects of relatedness and within-category position in the RT model (see Table 4.2 for all *Wald* χ^2 and *p* values). Participants were slower to respond to weakly-associated targets, and also showed slower categorisation towards the end of each category (i.e., within-category decline in performance). The model also revealed three significant interactions (see Figure 4.3) between:

- (i) Relatedness and within-category: Participants made slower responses towards the end of each category for strong items, while responses were faster for weak items towards the end of each category.
- (ii) Relatedness and eyes closed vs. open: Participants were faster for both strong and weak items in the eyes open condition compared to the eyes closed condition but the effect of strength of association appeared to be somewhat greater in the eyes closed condition.
- (iii) There was a marginally significant interaction between all the predictors – Eyes closed vs. open, sham-anodal, relatedness and within-category position ($p = .051$): Response times were overall faster in the anodal compared to sham stimulation (see Figure 4.3). In the eyes closed condition, this effect was particularly evident in the categorisation of weak items in the first half of each category, when participants found it harder to retrieve weakly associated items, and towards the end of the category for strong items, when activation of previously categorised strong items slows responses, as in the sham condition. In the eyes open condition, anodal stimulation benefited performance across all conditions; these effects were further explored based on the congruency of items in the next model.



Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals



Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals.

Figure 4.3: Mean response times (ms) for the strong and weak targets in the first half and second half of each category (within-category fatigue), comparing performance in the sham and anodal conditions, and shown individually for the eyes closed and eyes open conditions.

2. Eyes open: Congruent vs. Incongruent conditions

The effects of the following fixed within-subjects factors were examined in a repeated-measures GLM: (a) *congruent-incongruent* (performance on trials with pictures congruent or incongruent to the auditory items), (b) *sham-anodal* (performance split by trials with sham stimulation compared with anodal stimulation), (c) *relatedness* (strong vs. weak items), and (d) *within-category* position (comparison of task performance in the first half compared with the second half of each category). The *day of testing* (i.e., day 1 or 2 of testing) was also modelled without interaction terms, to capture all aspects of the design. Separate models were run on: (1) *response sensitivity* and (2) *response times*, including baseline performance and average RT/sensitivity as a covariate respectively. As before, the GLM started with a fully factorial model (i.e., taking all predictors and interactions into account). Only significant interactions from the previous model were entered into the next model, finally building a model which provided the best fit, measured using the quasi-likelihood information criterion (QIC), reported in Table 4.1. All significant *Wald* χ^2 and *p* values from the final model have been reported in Table 4.3. Pairwise contrasts for all *sham-anodal* comparisons presented in each figure have been reported in Table 4.4.

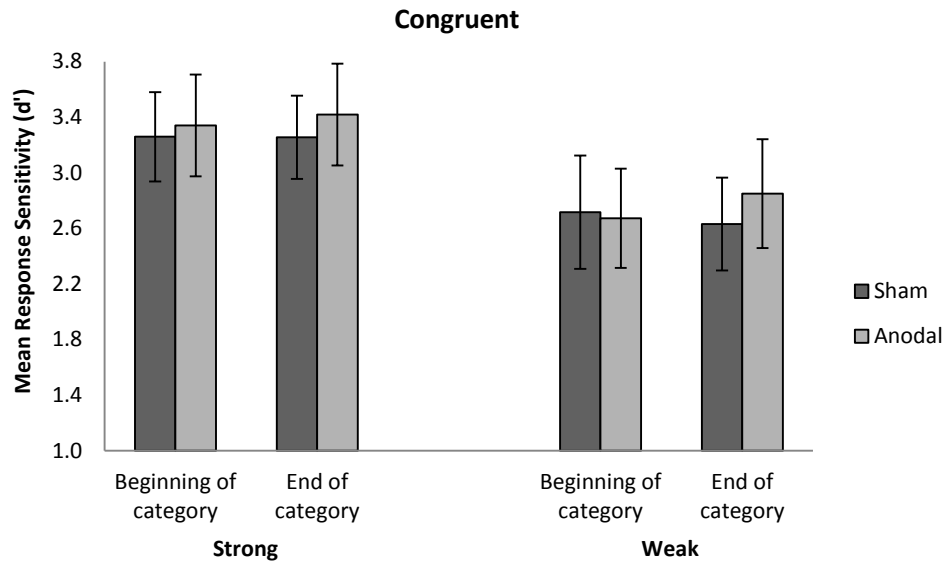
Table 4.3: Summary of significant results from the GLM analysis for the eyes open condition, split by performance on the congruent and Incongruent conditions – looking at the effects of congruency (congruent vs. incongruent), stimulation type (sham vs. anodal), relatedness (strong vs. open), and within-category performance, for the key dependent measures – response sensitivity and response times.

Eyes open: Congruent vs. Incongruent		
	Response Sensitivity	Response Times
Fixed effects:	Wald χ^2, <i>p</i>	Wald χ^2, <i>p</i>
Congruent-Incongruent	112.52, < .001	45.79, < .001
Sham-Anodal	<i>p</i> > .1	<i>p</i> > .1
Relatedness	157.88, < .001	164.67, < .001
Within-category	<i>p</i> > .1	<i>p</i> > .1
Significant interactions:		
Congruent-Incongruent x Relatedness	10.24, .001	8.02, .005
Congruent-Incongruent x Within-category	-	4.61, .032
Relatedness x Within-category	-	4.10, .043
Congruent-Incongruent x Sham-Anodal x Relatedness x Within-category	-	15.76, .046

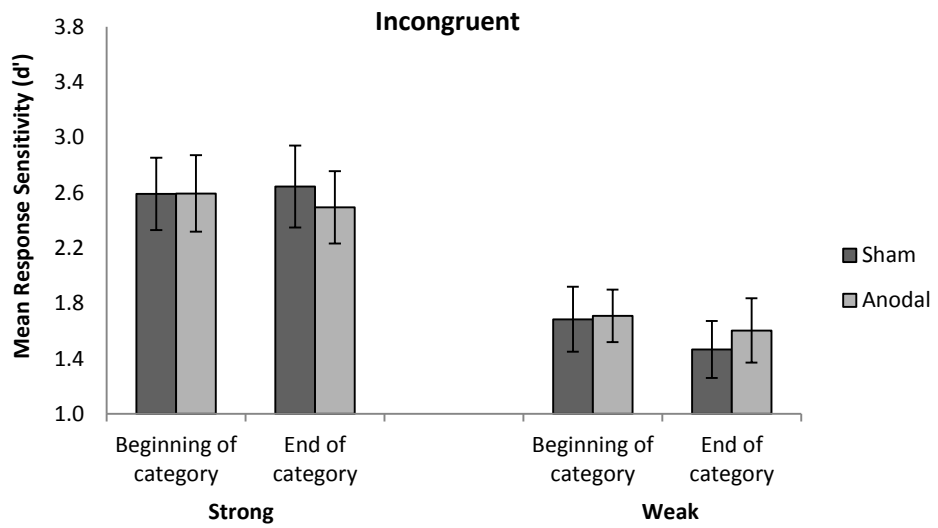
Footnote: Table presents two analyses employing (i) mixed effects modelling for response sensitivity (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest) and (ii) mixed effects modelling for response times (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed *d'* per category to be included as a covariate of no interest).

(1) Response Sensitivity

The congruency model also did not reveal any significant effects of stimulation, there were however significant main effects of congruency and relatedness (see Table 4.3 for all *Wald* χ^2 and *p* values), and a significant interaction between congruency and relatedness: Performance on trials paired with congruent pictures was better relative to the presentation of incongruent items. While the congruency of the pictures affected categorisation of both strong and weak associations, the effect of strength of association was greater for incongruent trials (see Figure 4.4).



Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals.



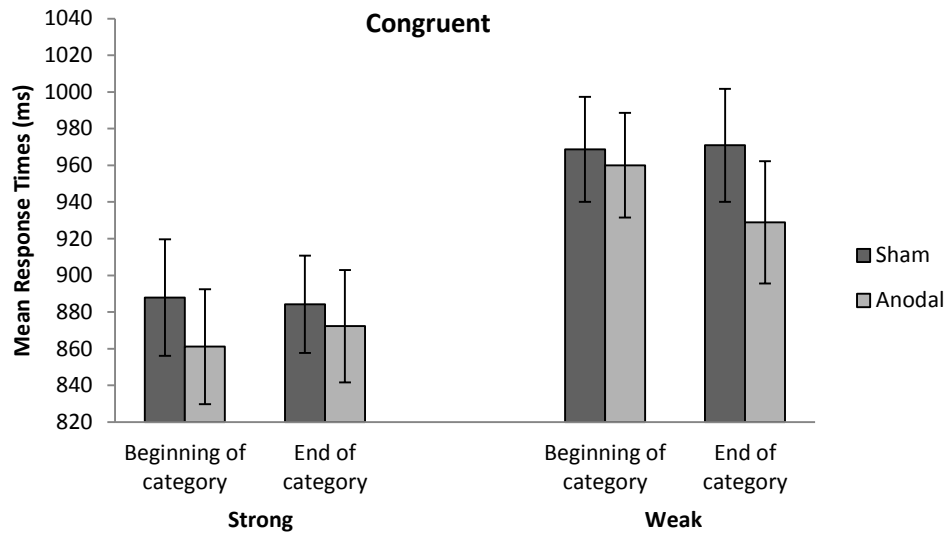
Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals.

Figure 4.4: Mean response sensitivity (d') for the strong and weak targets in the first half and second half of each category (within-category fatigue), comparing performance in the sham and anodal conditions, and shown individually for the congruent and incongruent conditions.

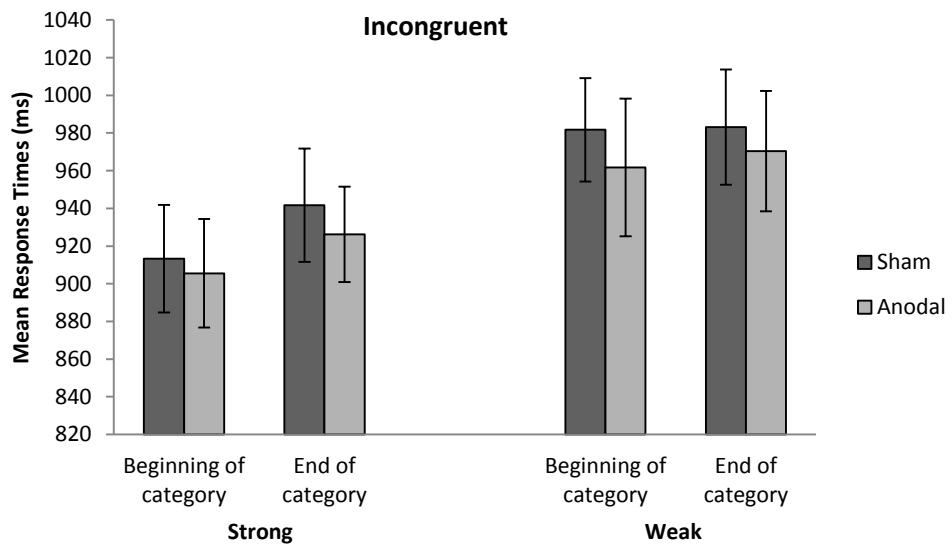
(2) Response Times

There were significant main effects of relatedness and within-category position in the RT model (see Table 4.3 for all *Wald* χ^2 and *p* values). The model also revealed the following significant interactions (see Figure 4.5):

- (i) Congruent-incongruent and relatedness: Participants responded faster to the strongly related targets, particularly in the congruent condition compared to the incongruent condition.
- (ii) Congruent-incongruent and within-category: Participants took longer to respond on trials presented with incongruent pictures, particularly towards the end of each category.
- (iii) Relatedness and within-category: Similar to the model including all the data above, participants responded more slowly towards the end of each category for strong items, while they made slightly faster responses towards the end of each category for weak items.
- (iv) Congruent-incongruent, sham-anodal, relatedness and within-category position: the incongruent trials showed the expected pattern of slower categorisation for strongly-related targets towards the end of each category, and this pattern was ameliorated by the application of anodal tDCS. However, in congruent trials, positive effects of stimulation were noted for weak items towards the end of the category, as would be expected if tDCS facilitated category-learning effects or the capacity to integrate congruent visual information in their classification of weak auditory associations (see Figure 4.5).



Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals.



Footnote: Plotted using estimated marginal means from the GLM analysis. Error bars show 95% confidence intervals.

Figure 4.5: Mean response times for the strong and weak targets in the first half and second half of each category (within-category fatigue), comparing performance in the sham and anodal conditions, and shown individually for the congruent and incongruent conditions.

Table 4.4: Pairwise comparisons presented for the dependent measures (response sensitivity and response times) and for the two models (eyes closed vs. open and congruent vs. incongruent); comparing performance for the sham and anodal conditions based on relatedness (strong vs. open) and within-category (beginning vs. end of category).

Pairwise comparisons (sham vs. anodal)					
		Response Sensitivity		Response Times	
		Eyes closed	Eyes open	Eyes closed	Eyes open
Strong	Beginning of category	.964	.841	.859	.359
	End of category	.950	.987	.351	.237
Weak	Beginning of category	.798	.943	.578	.370
	End of category	.949	.314	.880	.118
		Congruent	Incongruent	Congruent	Incongruent
Strong	Beginning of category	.750	.988	.256	.690
	End of category	.544	.511	.556	.330
Weak	Beginning of category	.864	.887	.674	.360
	End of category	.420	.416	.029	.555

Footnote: Table presents *p*-values of sham and anodal comparisons, computed using pairwise contrasts of estimated marginal means based on the original scale of the dependent variable (i.e., response sensitivity and response times) from the GLM analysis (using generalised estimating equations), for all-level combinations of the fixed factors, but reported here only for the key comparisons presented in figures.

Discussion

Previous studies have shown important contributions of LIFG in resolving competition and in the controlled retrieval of task- or context-relevant aspects of semantic meaning (Badre et al., 2005; Bedny, McGill, & Thompson-Schill, 2008; Gold, Balota, Kirchoff, & Buckner, 2005; Pisoni, Vernice, Iasevoli, Cattaneo, & Papagno, 2015; Schnur et al., 2009; Snyder, Banich, & Munakata, 2011; Thompson-Schill et al., 1997; Wagner et al., 2001; Whitney et al., 2009). In the current study, it was investigated if anodal stimulation of this region would impact categorisation in a demanding continuous auditory semantic categorisation paradigm, in which retrieval declines with repeated access to the same category. It was hypothesised that tDCS to LIFG might reduce this decline in continuous categorisation if retrieval becomes harder following the retrieval of related information, either from temporary increases in competition, or from the weakening of links between the probe category and other potential targets during the retrieval of each item. The study also examined the effect of tDCS to LIFG on two other manipulations more clearly linked to controlled semantic retrieval demands (classification of strong and weak associations) and the selection of relevant information (trials with incongruent visual distractors along with auditory targets). While there were no significant main effects of stimulation, there were

significant higher-order interactions that included tDCS. Results showed beneficial effects of anodal stimulation that were reflected in faster response times, although this effect emerged from complex interactions: beneficial effects were observed at different time points during testing, depending on both strength of association and whether participants had their eyes closed or open, and therefore whether distracting visual information was presented simultaneously:

(1) In the eyes closed task, the detection of weak targets at the beginning of the category was enhanced by tDCS in comparison to performance without stimulation. Weak associations are thought to require more controlled retrieval, and this might be particularly the case at the start of the category when relevant representations must be retrieved for the first time. In addition, tDCS facilitated the categorisation of strong items towards the end of the category. The decline in continuous categorisation is stronger for highly related targets (see Chapter 2) and this might reflect greater difficulties retrieving associations when a probe word has already been associated with similar targets previously. Stimulation of LIFG ameliorated this effect.

(2) In the eyes open task, categorisation was easier on trials in which the picture was congruent with the auditory stimulus. In the incongruent trials (in which an irrelevant visual stimulus was presented concurrently with the spoken word), the expected pattern of slower responses towards the end of each category was observed, and this pattern was ameliorated by the application of tDCS (much as it was in the eyes closed trials). For congruent trials, stimulation appeared to improve performance for weak associations towards the end of the category. The interpretation of this pattern is unclear but participants may have been better able to determine the relevance of the weak associations after practice on the category, and this category-learning effect may have been boosted by the electrical stimulation.

The finding of initial facilitation in the retrieval of weak associations is consistent with previous studies showing that the selection of weakly associated stimuli was improved when participants received anodal tDCS over LIFG compared to no stimulation (Lupyan et al., 2012). The benefit of tDCS for weakly-associated targets in the absence of repetition (i.e., at the beginning of the block) in the current study essentially replicates this effect. More generally, studies using tDCS over LIFG have found that participants were: (i) faster at deciding if a particular stimulus was coherent or incoherent (Cohen-Maximov et al., 2015), (ii) faster to retrieve the meanings of words with several meanings (Ihara et al., 2014), and (iii) also better at fluency in word generation tasks from specific categories (Lupyan et al., 2012). Overall, these results together with findings from this study provide evidence that the effortful retrieval of items is modulated by LIFG and can be enhanced using anodal tDCS.

While previous studies using tDCS have shown amelioration of the effect of maintaining semantically-related retrieval in word production paradigms, including continuous naming paradigms and tasks involving the cyclical repetition of items (Meinzer et al., 2016; Pisoni et al., 2012; Wirth et al., 2011), evidence for these effects was found in a comprehension task. In addition, since the task did not repeat stimuli, as in the case of semantic blocking paradigms, it suggests that stimulation to LIFG either modulated the capacity to control retrieval relevant to each target, even in the face of growing competition (from previously-presented and semantically-linked items) or following increased difficulty with retrieval that might reflect the suppression of alternative associations to a probe category to facilitate retrieval of each successive target, which would weaken performance later in the block. In other words, the retrieval of an association between PICNIC and “*rug*” might require the temporary suppression of “*sandwich*”, to enable the target word to efficiently drive the current decision (Oppenheim et al., 2010; see also Anderson, Bjork, Bjork, & Jordan, 2000). LIFG might allow later targets to be retrieved rapidly despite this increasing effect. In the study as a whole, it was found that tDCS to LIFG supported situations where the demands on controlled semantic retrieval were maximal, as observed in faster response times relative to sham, but there was less evidence that stimulation supported selection per se, since there was no evidence that tDCS particularly benefitted performance in the incongruent trials, when distracting visual information had to be ignored.

In addition, positive effects of anodal tDCS were also noticed in the congruent condition: participants made use of congruent information in detecting weaker associations over the course of the category, suggesting a possible benefit of tDCS for category learning. Although the application of tDCS has been used in the fields of memory and learning (Kincses, Antal, Nitsche, Bártfai, & Paulus, 2004; Liuzzi et al., 2010; Meinzer et al., 2014; Savill et al., 2015), very few studies have looked at the effects of tDCS on learning a semantic category, and this finding warrants further investigation.

Chapter 5

Discussion

Summary of results

Semantic cognition provides the basis for our successful retrieval of meanings and allows us to use this knowledge to interact with items in our environment in a flexible, context dependent way (Jefferies & Lambon Ralph, 2006). While it is known that retrieval of items from memory can be improved with repetition (Radeau, Besson, Fonteneau, & Castro, 1998), for example, the word CAT primes the word DOG due to automatic spreading activation between associated concepts (Badre & Wagner, 2002; Neely, 1977), there is also evidence that repetition of stimuli can cause paradoxical changes to occur in their meaning. These effects have been reported in both: (i) patients with semantic aphasia, where comprehension declines when semantically related items are repeated in cyclical matching tasks ('refractory effects'; Jefferies & Lambon Ralph, 2006), and (ii) in healthy participants, where multiple presentations of the same items can lead to subjective changes in the meaning that a particular stimulus conveys, as seen in 'semantic interference' effects (e.g., Belke, Meyer, & Damian, 2005), and/or 'semantic satiation' paradigm (e.g., Balota & Black, 1997). Although these effects are most commonly seen in language production tasks, they have been reported to depend on processes operating at a conceptual level (e.g., Belke, 2013); this would suggest that declining performance in semantic categorisation tasks might be observed even without the repetition of individual items in semantically-related sets. Thus, one of the key aims of this thesis was to explore if the accessibility of conceptual knowledge declines over time even without stimulus repetition, and the circumstances that increase or decrease this effect, in healthy young participants in **Chapter 2**, and in patients with semantic aphasia (SA) and age-matched controls in **Chapter 3**. Lastly, the role of LIFG in semantic control processes was investigated using evidence from brain stimulation (tDCS) in **Chapter 4**.

In each chapter, difficulties in categorisation were assessed using a paced serial semantic task (PSST). In this task, participants were presented with a stream of inputs and were required to press a button every time they detected a target that matched a particular category. Neither targets nor distracters were repeated but the paradigm involved sustained attention and a degree of flexibility in categorisation. The task considered the ability of participants to sustain semantic processing over time: both *within* categories – by examining whether comprehension declined over the course of each category as more related targets were presented, and *between* categories – by quantifying changes in performance across the experiment, as participants became fatigued. Various other manipulations within the PSST paradigm allowed for the assessment of other

aspects of semantic control, such as the ability to categorise items based on their *strength of association*, (e.g., HOSPITAL: strong, “doctor”; weak, “bone”; or unrelated, “Captain”).

Retrieval-related declines in categorisation in healthy young adults were assessed across five experiments in **Chapter 2**. In each experiment, participants’ performance declined towards the end of the category, and a release from this semantic decline was observed following a switch to a new category, demonstrating that this was not a general effect of time on task. The decline in categorisation was greater for target words that were strongly-associated with a thematic category (e.g., the item “sandwich” for the category PICNIC), as opposed to weakly-associated (e.g., the item “wasp” for PICNIC). The effect was eliminated when decisions could be made at a slower presentation rate, and a decline in comprehension was also observed across modalities when word and picture stimuli were interleaved. This study also examined potential effects of the classification judgement required: classification of items was contrasted based on thematic categories (PICNIC), taxonomic categories (e.g., FRUITS – “apple”, “banana”, “orange”), and categories defined by a single feature selected to be the current goal (e.g., colour GREEN – “spinach”, “frog”, “jade”). All of these tasks elicited similar retrieval-dependent declines in categorisation. The final experiment in Chapter 2 increased control demands by incorporating a secondary task within the PSST paradigm. This increased the magnitude of within-category decline. Thus, across five experiments it was found that, in healthy participants, the ability to retrieve specific meanings declined as a consequence of sustained semantic retrieval of items relevant to a particular conceptual goal. The accessibility of representations of meaning was found to change in a dynamic fashion as a consequence of the nature of ongoing cognition.

Chapter 3 considered how ageing and semantic aphasia may influence declining performance on the PSST paradigm, since the capacity to employ semantic control to tailor semantic retrieval to a specific goal may be compromised in patients with semantic control deficits (who typically had lesions of LIFG) and may also be weaker in older adults relative to younger volunteers. Depending on the mechanisms underpinning the within-category decline in categorisation, different effects would be expected in these groups: if retrieval-dependent declines in comprehension occur due to a build-up of competition, SA patients might have difficulty resolving this competition and therefore show an increase in within-category decline in categorisation. In contrast, if retrieval-dependent declines in comprehension are a consequence of successfully dealing with competition on earlier trials (cf. Anderson, Bjork, Bjork, & Jordan, 2000), these patients would not be expected to show this pattern, since their retrieval is relatively uncontrolled (e.g., Crutch & Warrington, 2005). The results showed that both patients with SA

(relative to age-matched controls) and older adults (relative to younger adults) were less efficient at retrieving weak associations, relative to stronger ones: in this way, both groups appeared to have weakened controlled retrieval of semantic information. In addition, neither group showed the within-category decline for strong associations seen repeatedly in healthy young participants in Chapter 2. Additionally, the PSST paradigm allowed the examination of whether there is a relationship between post-stroke fatigue and cognitive impairments producing difficulties sustaining attention to language in participants with aphasia. A fatigue visual analogue scale (F-VAS) was used to assess the subjective feelings of fatigue at different time points during PSST testing. Some patients showed an overall pattern of declining comprehension over the session, which correlated with their subjective feelings of fatigue. However, semantic control deficits and fatigue were independent in the sample. Therefore, fatigue in aphasia post-stroke was not likely to be a consequence of the increased effort required for sustained language processing in this group of patients.

Chapters 2 and 3 suggested that control processes play an important although complex role in within-category declines in comprehension. Drawing on the retrieval-induced forgetting literature, it might be that the application of control to inhibit competitors in early trials within each category gives rise to this pattern of retrieval-dependent decline in categorisation. However, the capacity to employ control in a flexible way might also be critical in overcoming the effect of retrieval-induced forgetting on later trials. The study in **Chapter 4** examined the effect of increasing the contribution of the left inferior frontal gyrus (LIFG) to semantic categorisation in the PSST, in healthy participants, through the application of anodal transcranial direct current stimulation (tDCS) to this region. LIFG has been associated with controlled access to semantic knowledge and conceptual selection; this region is also typically damaged in patients with semantic aphasia. The study investigated whether anodal tDCS to LIFG would modulate semantic control processes and aid categorisation on the PSST paradigm. Since LIFG is thought to support both controlled aspects of semantic knowledge (e.g., weak associations) and selection of conceptual knowledge from a field of strongly activated distractors, it was investigated how the effects of tDCS would interact with task manipulations loading on these aspects of semantic cognition: the strength of association of targets (strong vs. weak) was varied, since weak associations are thought to require more controlled retrieval, and the presence or absence of visual distractors was manipulated in an auditory decision task by including a congruency factor (participants were shown pictures, either congruent or incongruent to the auditory items). Positive effects of tDCS stimulation were observed in the response times of the participants, and benefits were dependent on the various conditions of the PSST paradigm. Categorisation of weak

items was enhanced at the beginning of categories, when it was hardest to retrieve less common associations. Performance for strong items was enhanced by tDCS towards the end of the categories; thus stimulation ameliorated the decline in continuous classification observed within categories in all of the experiments presented in the thesis that used young adults as volunteers. Finally, tDCS augmented learning effects in categorisation, particularly when congruent visual images were presented alongside the spoken words. Together these results constrain accounts of the role of LIFG in semantic retrieval and build on literature suggesting that stimulation of this region can facilitate conceptual retrieval. Next, findings from these chapters will be discussed in relation to the research themes and theoretical conclusions, and future directions.

Theme 1: Retrieval-induced declines in semantic cognition

Evidence from previous research suggests that repeatedly retrieving one aspect of knowledge suppresses related concepts, either using repeated presentations of the same items (as targets or as distracters; Campanella & Shallice, 2011; Harvey & Schnur, 2015; Wei & Schnur, 2015), or when these concepts are probed in a novel way (e.g., Anderson et al., 2000). However, it is unclear what determines whether semantic similarity will produce declines in comprehension or conceptual retrieval, and when these effects would emerge. These are some of the many factors that remain debated, and have been examined below based on the first set of findings from Chapter 2:

1. **Does the effect emerge in the absence of repetition of specific items?** Across five experiments in Chapter 2 the ability of participants to sustain semantic processing over time was considered: both *within* categories (i.e., examining whether comprehension deteriorated over the course of each category as more related targets were presented), and *between* categories (i.e., by quantifying changes in performance across the experiment, as participants became generally fatigued). Findings from this chapter demonstrated a cumulative decline in semantic categorisation – which occurred when decisions were made within a particular semantic category at a rapid rate, even *without the repetition of individual items*. These effects were not equivalent to time-on-task and could not be explained in terms of a general decline in sustained attention as a result of fatigue, as many categories were tested back-to-back over the course of the experiments and there was a release from deteriorating categorisation at category boundaries, i.e., when targets were no longer related to recently-categorised targets. The within-category effect resembled both declining comprehension in patients with semantic access deficits (e.g., Gardner et al., 2012; Jefferies et al., 2007; Thompson et al., 2015; Warrington &

Crutch, 2004), and similar effects seen in healthy participants when semantically-related items are categorised (Campanella & Shallice, 2011; Harvey & Schnur, 2015; Wei & Schnur, 2015) – however, it occurred without the massed repetition of individual items that was common across all the experiments. These findings thus add to the growing body of evidence that conceptual processing can become less efficient following retrieval of semantically related items.

2. **Could the effects be explained by a change in response bias or category learning?** Over the course of a category, participants might learn about the range of targets (their rates of misses and/or false alarms might decline), or they might be genuinely less able to discriminate between targets and distractors following retrieval of related targets (i.e., there might be a change in d' , reflecting a rise in hits plus a reduction in false alarms). Within-category decline effects in Chapter 2 were consistent and observed across two different paradigms: a vigilance paradigm, in which participants attempted to detect targets that were less frequent than distractors (i.e., 20 targets along with 40 distractors in each category), and also in a 2AFC paradigm where target and distracter items within and outside of the target category were presented equally often (i.e., 20 targets and 20 distractors). Further examination of this using cross-experiment comparison indicated a cumulative decline in the number of hits within each category, with no substantial change or increase in participants' rate of false alarms from the beginning to the end of each category. This confirmed that participants were less able to categorise accurately towards the end of each category, and were not simply changing their response criteria following more experience with each category. These results thus suggest that the within-category decline effect is not due to a change in participants' criteria for category membership; rather it is more likely to occur because of an increasing inability to identify the targets and reject the non-targets.

3. **Does the effect require strong global relationships between targets (as in the aphasia refractory paradigm) or does it influence the accessibility of goal-relevant features?** The latter prediction would suggest the effect emerges not from a pattern of automatic spreading activation between related concepts that need to be controlled later on, but instead from the way in which control may be applied to retrieve specific goal-relevant information, even if these are features – as through the process of retrieving one item that has a particular feature, other items with this feature may need to be suppressed.

The findings showed that global semantic relationships between targets was not required for this effect, as within-category decline was seen across: taxonomic (e.g., VEHICLES: “car”, “bus”, “truck”), thematic (e.g., HOSPITAL: “doctor”, “bed”, “bone”), and individual feature-based classification (e.g., colour RED: “tomato”, “post-box”, “Santa”), suggesting that this pattern is a fairly ubiquitous consequence of sustained semantic retrieval, at least in circumstances such as those created by the PSST paradigm, where the focus of retrieval is pre-defined and not permitted to evolve over time. The observed effects therefore emerged not from strengthening activation in sets of globally-related concepts, but instead reflect interactions between semantic goal representations (for example, are targets: ‘thin’, or ‘red’, or ‘round’) and the conceptual store.

4. **Is it a lexical effect, or a lexical-semantic effect, or a conceptual effect?** Within the literature on semantic access impairment, there has been debate about whether declining comprehension is restricted to auditory-verbal materials (Crutch & Warrington, 2008; Warrington & McCarthy, 1983; Warrington & Crutch, 2004), or whether it extends to non-verbal tasks (Forde & Humphreys, 1997; Gardner et al., 2012; Thompson et al., 2015). Similarly, opposing psycholinguistic studies have argued that semantic interference effects reflect lexical processes (e.g., Damian et al., 2001) or alternatively conceptual processes that extend to picture matching tasks (Wei & Schnur, 2015). But since theories suggest that amodal conceptual knowledge interacts with modality-free semantic control processes, these effects could perhaps be generalised across modalities (Patterson, Nestor, & Rogers, 2007; Rogers et al., 2004; see also Wei & Schnur, 2015). Results from this chapter indicated that declines within each category in comprehension extended beyond auditory-verbal stimuli to include categories in which semantically related word and picture stimuli were interleaved, suggesting that these results are unlikely to reflect either effects at a lexical-level or effects within the mappings between concepts and specific inputs. Therefore, this phenomenon originated within amodal conceptual representations that were not specific to a particular input modality.
5. **Is it a fast or slow effect?** Fast decisions may be more vulnerable if more selection has to be employed (in the face of too much activation of competitors) or if the demands on controlled retrieval are great (if the target has been inhibited and is therefore relatively inaccessible without control). This is because the application of top-down control processes to semantic retrieval may take time to produce a different pattern of

conceptual activation. It is still feasible that the effects may last a longer time (i.e., extend to occasional targets presented in a stream of non-targets). It was found that the within-category decline in categorisation was indeed sensitive to presentation rate: it was stronger when rapid processing was required. This effect resembles previous findings which show deteriorating comprehension for repeated items in semantically-related sets when healthy participants had to respond by a deadline (Campanella & Shallice, 2011). Sensitivity to speed of response suggests that this effect might reflect a process that takes time to resolve – such as narrowing the pattern of retrieval to focus on information relevant to the target.

6. **Lastly, does the effect arise as a consequence of a build-up of competition, or a build-up of inhibition (to control competition on earlier trials)?** These predictions make opposite suggestions about the strength of association in a continuous categorisation task, since weak items should experience more competition from irrelevant activated information, while strong items should accrue more suppression during the retrieval of earlier targets. Within-category decreases in chapter 2 were greater for targets strongly-associated with the category label (e.g., PICNIC – “sandwich”), compared with weakly-associated targets (e.g., PICNIC – “wasp”). Furthermore, the requirement to respond rapidly within a condition was contrasted in which there was more time for retrieval; however, the lag between successive targets was not manipulated and the cumulative decline in categorisation was unlikely to be very short-term since the targets were interspersed with distractors. Thus, it can be proposed that the effects observed are compatible with a build-up of conceptual interference (as reported by Wei & Schnur, 2015), combined with a retrieval process for each item that takes time to resolve, meaning that participants were less likely to settle on the correct response when there was little time to respond, following the build-up of conceptual interference towards the end of each category (see below).

One way of considering the effects of compromised categorisation following sustained semantic retrieval focussed on a specific category can be explained in terms of the ‘cue-overload effect’ (Watkins & Watkins, 1975). Research on this phenomenon has shown that when many different associations to a given item are encoded or primed, this can interfere with the ability to recall each of these links, presumably due to reductions in the efficiency with which the cue can re-activate the target and the existence of many possible associations that can be retrieved from

the cue. The PSST paradigm characterised the *immediate* effects of previous retrieval on evolving performance, as opposed to the subsequent effects of having many activated associations during later recall. Towards the end of each category, when performance was poorer, there may have been more interference with the classification of new targets, following the priming of other goal-relevant representations (reflecting residual activation of previous targets or, perhaps more likely given the nature of the task, weight changes between the category goal and previous targets). This made it more difficult to identify the relationship between a newly-presented item and the target category (especially when there was a short deadline to respond). For example, for the category PICNIC, previous targets “sunshine” and “rug” might have made the categorisation of a new item, “cake”, less efficient, since these items would have been previously associated with the goal and all of the items shared goal-relevant features; thus there may have been competition at the point of decision. Also the fact that the targets don’t have to be globally related perhaps suggests too much goal-related inhibition, as seen in retrieval induced forgetting (RIF), where retrieval depends on inhibitory mechanisms to overcome these interfering effects (see Anderson, 2003 for a review). RIF effects have also been found to affect strong associations more than weak exemplars of categories (Anderson, Bjork, & Bjork, 1994), as these items require more suppression due to greater activation between related items as opposed to weak associations, as is also evidenced in Chapter 2. Furthermore, the speed effect is potentially consistent with these theories but suggests that retrieval evolves over time and this process takes longer towards the end of the category, compatible with control mechanisms overcoming the retrieval-induced problems in categorisation. It can also be concluded that the effects might emerge from the interaction of domain-general control processes and amodal representations – as it extends across modalities – although the effect of semantic control is considered in the next section.

Theme 2: The effect of semantic control on retrieval-induced decline in categorisation

Contemporary accounts of semantic processing envisage that amodal concepts interact with control processes to support context- and task-appropriate semantic retrieval (Lambon Ralph, Jefferies, Patterson, & Rogers, 2016). Consequently, within-category declines in categorisation might show an influence of the capacity to control retrieval, although the nature of this influence is likely to depend on the underlying mechanism giving rise to deteriorating categorisation. By one account, categorisation becomes harder as more and more related conceptual representations are primed by their previous presentation, and this gives rise to competition. By this view, populations and manipulations that reduce the ability to selectively retrieve currently-relevant information in the face of strong competition should magnify the

effects of within-category decline. An alternative view suggests the retrieval of initial targets gives rise to the suppression of related information, and this makes subsequent targets less accessible (and potentially more demanding of controlled retrieval processes), such as the RIF effect. If this is the underlying mechanism, the effects of reduced semantic control are likely to be more complex. If initial retrieval is relatively uncontrolled (as in patients with semantic aphasia), earlier trials may trigger less suppression of related information, and thus the effect of within-category decline may be eliminated or attenuated. However, in populations who show strong within-category decline (e.g., healthy young adults), this effect may be increased in magnitude by manipulations that reduce the capacity for control (i.e., divided attention in a dual task paradigm), as well as reduced by manipulations that increase the capacity for control (e.g., tDCS to LIFG), since retrieving relevant information after it has been inhibited on earlier trials is likely to draw more strongly on control process.

In Chapter 2, the within category decline effect for strongly-associated targets was increased in participants by a secondary task that divided attention. This effect is potentially compatible with both of the theoretical accounts outlined above, since ongoing task-irrelevant activation for related items may have increased demands on selection, while the suppression of related information from earlier trials might also have increased the controlled retrieval demands of later trials when this suppressed information had to be accessed. Thus, to be able to completely decide between these accounts, the effects in older adults and SA patients was examined in Chapter 3, as both groups have reduced capacity for semantic control. It is possible that older adults and SA patients may have particular difficulties detecting relationship between category labels and *weak* targets on the PSST, since understanding the relevance of weak semantic associations is thought to require stronger engagement of controlled retrieval mechanisms (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). Furthermore, results from patients with SA may help explain the previous findings in two ways: SA patients would either benefit on later trials if their initial retrieval is uncontrolled, i.e., eliminating the possibility of RIF; or their performance would decline over the course of the category if the effects observed in Chapter 2 are a consequence of growing competition, as SA patients have difficulties suppressing irrelevant aspects of knowledge (Noonan, Jefferies, Corbett, & Lambon Ralph, 2010).

Both older adults and SA patients did not show declining categorisation for strong targets in Chapter 3, however both of these groups showed poor semantic control, in that weak associations were less accessible than strong associations – i.e., patients with SA were more impaired at weak vs. strong trials, and older adults also showed a bigger difference between these

conditions than younger adults. This suggests that in populations with less controlled semantic retrieval the effect of within-category decline may be ameliorated: thus, it may be a consequence of applying control to support retrieval in earlier trials, which results in the suppression of potentially distracting information, and patients with SA and older volunteers do this less.

This is further supported by previous work suggesting that both older controls and patients with SA retain conceptual information but have difficulties retrieving this information: (i) age associated deficits in retrieval mechanisms have been established using verbal fluency, object naming and semantic categorisation tasks (Baciu et al., 2016), and similar conclusions from meta-analysis and longitudinal studies of production tasks have shown age-related declines in picture naming (Feyereisen, 1997; Kemper, Thompson, & Marquis, 2001; Wierenga et al., 2008). Results from these findings have been attributed to decreased efficiency of executive functions (Baciu et al., 2016). In addition, studies have also shown decreased connectivity in the default mode network with aging (Biswal et al., 2010; Damoiseaux et al., 2008), and aspects of the semantic network implicated in retrieving associations are found within the DMN regions (Davey et al., 2016; Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015; Jackson, Hoffman, Pobric, & Lambon Ralph, 2015). Moreover, semantic cognition is thought to emerge from the interaction of multiple neurocognitive components, including the conceptual store in the anterior temporal lobes (ATL) and control processes that shape semantic retrieval in the left prefrontal cortex (Jefferies, 2013; Noonan, Jefferies, Visser, & Ralph, 2013), and studies have reported reduced activation in these regions during memory retrieval in older compared to younger adults (Grady et al., 1995; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Stebbins et al., 2002), making control processes more vulnerable with ageing. Thus, the disproportionate impact of ageing, as seen in the absence of within category decline for strong targets suggests that deficits in control mechanisms during initial retrieval reduce the need to suppress competitors on later trials, thus maintaining classification within categories. However, these deficits in control mechanisms also meant difficulties in retrieving weakly associated targets.

(ii) SA patients show difficulties when non-dominant semantic features or associations are required and when strong but irrelevant aspects of knowledge must be suppressed (Noonan et al., 2010). These patients thus have difficulty making connections between items that are further apart in semantic space (e.g., *chipmunk* with *bee*) than between more similar items (*chipmunk* with *squirrel*; Noonan et al., 2010). Findings from Chapter 3 similarly show that SA patients had greater deficits in controlled retrieval, i.e., they maintained close-to-normal performance for strong associations, compared to older controls, but had additional difficulties identifying weakly

associated targets. Therefore, their deficits in controlling activation of related information within each category eliminated the RIF effect, as opposed to causing increasing competition. These findings therefore contrast performance on cyclical tasks, where SA patients are reported to show 'refractory' effects – i.e., declining comprehension when items are presented repeatedly (Gardner et al., 2012; Jefferies et al., 2007; Thompson et al., 2015), even though their deficits in semantic control meant a reduction in the decline or RIF effect on PSST. One possibility for this could be that these effects reflect different mechanisms – for example, in the cyclical paradigm, there is the potential for ongoing activation in a very simple task and so the structure of the task is designed to maximise competition. In a continuous paradigm, including the PSST, targets are distributed amongst many distractors and so the structure of the paradigm is set up to detect slightly longer-term effects, and it is more likely that there will be RIF effects. This was further examined in the next section, i.e., whether deterioration in 'refractory' task over repeated trials is connected to cognitive fatigue, or if performance on this task could be linked to the difficulty of sustaining specific focus for semantic retrieval (i.e., whether patients showing 'refractory' effects would also show within-category decline on the PSST relative to other patients in the group).

Lastly, the pattern of decline seen in the dual task study and SA patients is inconsistent with previous studies that have used dual task methods to simulate SA performance (Almaghyuli, Thompson, Lambon Ralph, & Jefferies, 2012). More research is needed to establish why manipulations of control sometimes increase the effect and sometimes decrease it. However, it appears that this ability might depend on the extent to which participants are attempting to use a controlled retrieval strategy.

Theme 3: Post-stroke fatigue and aphasia

While findings from Chapter 3 are consistent with a deficit of semantic control in SA patients, other effects were also investigated, i.e., concerning the relationship between the deregulation of semantic retrieval and mental fatigue post-stroke. Many people with post-stroke aphasia experience cognitive fatigue – i.e., a sense of exhaustion after effortful language, cognitive and/or social processing – and this can be debilitating even for stroke survivors who have otherwise made a full recovery (Staub & Bogousslavsky, 2001). The relationship between fatigue and aphasia has rarely been examined, yet the capacity to maintain a central focus for semantic cognition could be related to this difficulty. Discussion of this issue is important, because fatigue is potentially detrimental to physical and psychological recovery after stroke. Fatigue poses one of the greatest barriers to rehabilitation and has negative impact on quality of life as it often interferes with the rehabilitation processes and impairs the patients' ability to regain

functions lost because of the stroke (Crinion, Holland, Copland, Thompson, & Hillis, 2012; Pedersen, Vinter, & Olsen, 2004; Wade, Hower, David, & Enderby, 1986). Most studies have used multidimensional self-reported questionnaires to measure post-stroke fatigue (Lynch et al., 2007), however, it is also not clear if patients always have insight into the effects that fatigue might have on their cognitive performance. Chapter 3 attempted to explore this along with performance on the PSST paradigm, and used a fatigue visual analogue scale (F-VAS; “0” – ‘not at all tired’ to “10” – ‘extremely fatigued’) to examine the patients’ subjective feelings of fatigue and if their levels of fatigue interacted with their performance.

It is plausible to assume that for individuals with greater semantic and/or executive impairment, cognitive tasks are more tiring and this gives rise to mental fatigue. However, no evidence was found that more severely impaired cases showed greater decline in performance across the session. Chapter 3 also examined the relationship between fatigue, declining categorisation on the PSST and refractory effects. ‘Refractory’ performance was assessed in cyclical matching tasks, since these are a hallmark of semantic access impairments – when the same items were presented repeatedly across a number of cycles, matching accuracy fell, and it was further explored if performance on this task would correlate with PSST performance and ratings of fatigue. Refractory effects were associated with difficulty identifying *weak* targets on the PSST, consistent with the perspective that suggests this pattern reflects semantic control impairment (Badre & Wagner, 2007; Forde & Humphreys, 1995, 2007; Jefferies et al., 2007). Even though refractory deficits involve declining comprehension over time (with release from this effect when the set of items is changed); there was no discernible correlation with fatigue in this chapter – either with the fall in performance over blocks across the session, or with subjective feelings of mental tiredness. This suggests that semantic control deficits and fatigue are broadly independent. Moreover, fatigue ratings correlated with the decline in comprehension for weak items over the course of the task, so patients appear to have some insight into their declining comprehension. These findings further elucidate the nature of the semantic impairment in SA and establish that while both mental fatigue and deficits of controlled semantic retrieval are common consequences of stroke, they are not likely to have a common cause.

Theme 4: Semantic control and the role of LIFG

The importance of semantic control processes within the PSST paradigm appear to be greater on later trials, i.e., with the need to overcome previously induced inhibition of related associations, however, this requirement seems to depend on the initial application of control to guide categorisation. In neuroimaging studies, activity in the left inferior frontal gyrus (LIFG) has

been particularly associated with controlled access to semantic knowledge, when the link between the probe and target is weak, and circumstances where there is competition and high selection demands (Badre et al., 2005; Nagel, Schumacher, Goebel, & D'Esposito, 2008; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Maril, Bjork, & Schacter, 2001). The role of this region has also been proposed in several semantic interference accounts, concerning domain-general and top-down control mechanisms (Belke & Stielow, 2013; Oppenheim, Dell, & Schwartz, 2010; Schnur et al., 2009). Furthermore, recent studies have shown that electrical enhancement of LIFG using transcranial direct current stimulation (tDCS) improves lexical retrieval and reduces accompanying activation of LIFG, and also increases the connectivity of this region with other brain areas underlying the language network (Meinzer et al., 2012; Meinzer, Yetim, McMahon, & de Zubicaray, 2016). This could possibly reflect strengthening of top-down control processes following LIFG stimulation. In Chapter 4 the PSST paradigm was used to examine the effects of tDCS to LIFG in healthy young participants, on multiple potentially interacting factors, that are thought to influence semantic control, i.e., controlled retrieval and selection demands.

Controlled retrieval

Stimulation effects were compared for the within-category decline (i.e., performance in the first half and second half of each category), since controlled retrieval demands may be initially high (in the absence of priming of semantically-relevant features). The strength of association between the probe category and the target was also manipulated, since controlled retrieval demands are higher for weakly-associated targets, and this effect would be particularly clear towards the beginning of each category. These predictions are supported by findings in Chapter 3, where semantic control deteriorated in older age and especially in patients with SA. This effect was directly associated with a difficulty in categorising weakly associated targets, and also resembled the effect of performance in the dual-task experiment in Chapter 2 where within-category decline was similarly affected when executive capacity was reduced, and classification of strong items showed a substantial effect of within-category decline under these conditions. Thus, it was envisaged that tDCS could boost the retrieval of weak associations initially by modulating control mechanisms, but later have a more protective effect on the retrieval of strong associations by preventing decline during the continuous categorisation. Findings from Chapter 4 were consistent with these predictions: detection of weak targets at the beginning of the category was enhanced by tDCS in comparison to performance without stimulation. Initial facilitation in the retrieval of weak associations are also consistent with previous studies showing that the selection of weakly associated stimuli is improved with anodal tDCS over LIFG compared to no stimulation

(Lupyan, Mirman, Hamilton, & Thompson-Schill, 2012). The benefit of tDCS was found for weakly-associated targets in the absence of repetition (i.e., at the beginning of the block), which essentially replicates this effect. Additionally, tDCS also facilitated the categorisation of strong items towards the end of the category. The decline in continuous categorisation was stronger for highly related targets seen in Chapter 2 (which reflected greater difficulties in retrieving suppressed associations that had already been associated with similar targets previously) – this effect was ameliorated by stimulation, further constraining the role of LIFG in semantic retrieval and that stimulation of this region can facilitate conceptual retrieval.

Selection demands

The role of LIFG has also been established in tasks requiring high selection demands, such as the resolution of lexical ambiguity (Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1997), and also in tasks with low selection demands yet requiring effortful retrieval (e.g., generating verbs from concrete nouns, Martin & Cheng, 2006), thus establishing the role of LIFG in top-down control processes that are required in selection (e.g., Heim, Eickhoff, Friederici, & Amunts, 2009). Further manipulations were therefore made in Chapter 4, by presenting distracting visual information during auditory semantic categorisation, i.e., auditory targets were presented concurrently with relevant or irrelevant images to determine whether tDCS to LIFG would boost selective retrieval driven by the auditory input and ameliorate the effects of visual distractors. Findings showed that categorisation was easier on trials in which the presentation of pictures was congruent with the auditory stimulus. In the incongruent trials (when an irrelevant visual stimulus was presented concurrently with the spoken word), expected pattern of slower responses towards the end of each category was observed, and this pattern was ameliorated by the application of tDCS (much as it was in the trials without the presentation of visual distractors). For congruent trials, stimulation appeared to improve performance for weak associations towards the end of the category. The interpretation of this pattern is unclear, but participants may have been better able to determine the relevance of weak associations after practice on the category with congruent images, and this category-learning effect may have been boosted by electrical stimulation, however, very few studies have looked at the effects of tDCS on learning a semantic category, and this requires further research.

Thus in Chapter 4 as a whole, it was found that while tDCS to LIFG supports situations where the demands on controlled semantic retrieval are maximal, there was less evidence that stimulation supported selection per se, as no evidence was found that tDCS particularly benefitted performance in the incongruent trials, when distracting visual information had to be

ignored. While previous studies using tDCS have shown amelioration of the effect of maintaining semantically-related retrieval in word production paradigms, including continuous naming paradigms and tasks involving the cyclical repetition of items (see Meinzer, Yetim, McMahon, & de Zubizaray, 2016; Pisoni et al., 2012; Wirth et al., 2011), Chapter 4 provided evidence for these effects in a comprehension task. In addition, since the paradigm used did not repeat stimuli, as in the case of semantic blocking paradigms, it suggests that stimulation to LIFG modulated the capacity to control retrieval that was relevant to each target, even in the face of growing task demands (i.e., from previously-presented and semantically-linked items). In other words, it could be that stimulation facilitated the increasing difficulty in retrieval due to the suppression of alternate associations to the probe category that weaken performance towards the end of each block, for example, the retrieval of an association between PICNIC and “sandwich” might require the temporary suppression of “cake”, to enable the target word to efficiently drive the current decision (Oppenheim et al., 2010; see also Anderson, Bjork, Bjork, & Jordan, 2000). LIFG might allow these later targets to be retrieved rapidly despite their interference effect.

Effects of control on within-category decline

Both studies with healthy young adults (i.e., dual task in Chapter 2 and tDCS in Chapter 4) have shown a pattern where increased control from brain stimulation reduces the effect of within category decline, while reduced control from dual task increases this effect. This might be because healthy young people have network connectivity that promotes top-down control on semantic retrieval, while older adults and SA patients show reduced within-category decline perhaps because they have brain connectivity that does not promote top-down control. Neuroimaging studies looking at functional or effective connectivity comparisons in young and older adults have shown such age related decreases in connectivity (Andrews-Hanna et al., 2007; Bennett, Sekuler, McIntosh, & Della-Maggiore, 2001; Cook, O'Connor, Lange, & Steffener, 2007; Damoiseaux et al., 2008; Sambataro et al., 2010), which subsequently compromise brain activation in older adults (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Grady, 1998; Reuter-Lorenz & Lustig, 2005; Schneider-Garces et al., 2010). This has been explained in terms of greater demands posed on executive control processes, which are known to be affected by structural brain deteriorations that occur with age (Grady, 2012). Further support for this comes from a tDCS study, where anodal stimulation to the LIFG modulated changes in connectivity and improved performance in older adults up to the level of younger adults in a word generation task (Meinzer, Lindenberg, Antonenko, Fleisch, & Flöel, 2013). Previous work with SA patients has also suggested that their deficits are associated with damage to left prefrontal and/or temporoparietal areas

consequent to stroke, hence producing difficulties retrieving information, particularly weak associations due to a failure of top-down control mechanisms over activation within the semantic store (Corbett, Jefferies, & Ralph, 2009; Noonan et al., 2010). Together, these studies confirm the evidence that top-down control from LIFG is necessary for the within-category decline in comprehension to occur in the first place, and that older adults and those with stroke to this region do not show within-category decline even though they clearly have an impairment of semantic control.

Based on findings overall, it can be concluded that control processes play an important although complex role in within-category declines in comprehension, which perhaps suggests two contradictory sides of semantic control: converging evidence from healthy participants in **Chapter 2** suggested that the application of control to inhibit competitors from early trials within each category gives rise to this pattern of retrieval-dependent declines in categorisation. While results from **Chapter 3** suggested that having little control may actually lead to better performance on later trials – together these findings point toward a ‘dark side of control’ (cf. Oppenheim et al., 2010). For example, although older adults were less able to efficiently retrieve weak associations, this allowed them better performance, as it meant that they did not experience increased difficulty with continuous categorisation, as otherwise it would have been more effortful to retrieve target relevant information that had been previously suppressed. However, evidence from **Chapter 4** proposed a more ‘light side of control’, in that enhancing control processes also improved categorisation, for both strong and weak associations, thus reiterating its important contributions in retrieval and classification demands in young participants. These findings have important practical implications, in particular, the finding that the accessibility of conceptual information may deteriorate through the earlier application of that information can be potentially beneficial in fields like education and speech and language therapy.

Limitations and future directions

While the present work sheds light on the contemporary accounts of semantic processing, and the underlying mechanisms of semantic control that supports context and task appropriate semantic retrieval, there are still a number of aspects that remain unclear or can be further investigated:

- Firstly, more work could be done to separate the “too much activation” from “too much suppression” accounts. For example, it could be informative to use lists in which there is strong competition at the start (as this should increase the within-category

decline effect if it reflects lateral inhibition to facilitate initial retrieval), contrasting with strong competition at the end. For instance, if the initial items included many harder weak associations, people would be expected to suppress dominant links even more to retrieve these items and then they might show the decline in categorisation very strongly for strong items. In contrast, if the initial items were largely easy (minimising competition), participants might not show the effects of decline as strongly.

- Further work is also needed to address when reductions in semantic control increase within-category declines in comprehension and when they reduce it, as a different pattern of performance was found under harder vs. easier dual task conditions in healthy participants (i.e., increased decline in comprehension with divided attention), and in SA patients with semantic control deficits relative to healthy controls (i.e., reduced decline in comprehension in SA). There were also different effects on the 'refractory' task and the PSST paradigm in SA patients. The mechanisms underpinning these effects may have differed, since the refractory paradigm focussed on resolving ongoing competition, while the PSST did not create strong competition between successive trials to the same degree. It would be useful to further differentiate the effects of control mechanisms on retrieval-related declines in comprehension.
- Although selection demands in the tDCS study were manipulated through the presentation of irrelevant visual distractors, this manipulation was not considered in the study with SA patients or older adults. This would have potentially helped understand the effects of tDCS better, particularly on incongruent trials.
- In addition, the role of semantic control processes in comprehension in older controls is not as well researched as in younger participants or SA patients, thus while the study begins to examine controlled retrieval deficits, further examination of the effects of visual distractors and/or the use of tDCS would have been useful.
- Neither neuropsychology nor tDCS have high spatial resolution and thus conclusions about brain regions need confirmation with more higher spatial resolution methods to look at the role of LIFG, and to also extend the investigations of the neural basis of this effect to other regions like pMTG, which is also implicated in semantic control (e.g., Krieger-Redwood & Jefferies, 2014).

- Findings in the tDCS chapter (Chapter 4) are unique in that it examined facilitation in categorisation without repetition or cyclical presentation of items; however, replication of these results is needed. The stimulation procedure involved the application of stimulation simultaneously with performance on the PSST paradigm. It would have been interesting to examine the duration of this effect. For example, there is some evidence that semantic fluency improved on a task 15 minutes post-stimulation (Penolazzi, Pastore, & Mondini, 2013); further examination of this in terms of comprehension could have implications in the formulation of stimulation protocols but also language therapies. Further research could also examine the effects of tDCS on learning a semantic category, leading to improved categorisation of weak associations in the congruent condition of PSST testing.

Conclusions

This thesis explores the factors that influence the accessibility of conceptual knowledge and examines its neural basis, by employing a paced auditory comprehension task that assesses the ability to retrieve specific meanings as a consequence of sustained semantic retrieval of items to a given conceptual goal. Findings from this research build on previous studies to show that there can be declines in comprehension even without repetition of individual items (**Chapter 2**). The accessibility of representations of meaning changes in a dynamic fashion ‘within’ each category, as a consequence of engaging strong semantic control on initial trials, and subsequently this effect appears to be attenuated in people who cannot control retrieval (**Chapter 3**). Declining performance in continuous categorisation thus appears to be a by-product of controlling competition when retrieving a related concept. The effect is strongest for strong associations in **Chapter 2**, which may have accrued more competition or inhibition. This was examined with SA patients (**Chapter 3**) who have control deficits, thus were either expected to show a stronger effect, if this is to do with failure to control competition from earlier trials, or a weaker effect, if this is to do with the use of control to suppress related information on earlier trials. Results from this thesis are compatible with the second view. Findings further suggest that this effect is attenuated by anodal tDCS to LIFG (**Chapter 4**), perhaps because this facilitates initial retrieval, by potentially reducing the inhibition of related information, and/or by strengthening subsequent target selection. These findings further constrain accounts of the role of LIFG in semantic retrieval and that stimulation of this region can facilitate conceptual retrieval. Lastly, this thesis also contributes to the current understandings of fatigue in aphasia post-stroke (**Chapter 3**) and

establishes that although mental fatigue and deficits of controlled semantic retrieval are common consequences of stroke, they do not appear to have a common cause

Appendices

APPENDIX A: Chapter 2 – When comprehension elicits incomprehension: Deterioration of semantic categorisation in the absence of stimulus habituation

Table 6.1: Signal detection scores for Experiment 1: Thematic-matching.

1.1 seconds	Within-category	Relatedness	Hits	Misses	False Alarms	Correct Rejections	<i>d'</i> score	Average RT (SD)
1 st half of session	1 st half of category	Strong	60.8	39.2	6.9	93.1	1.76	816.5 (40.9)
		Weak	51.4	48.6	6.9	93.1	1.52	875.6 (61.8)
	2 nd half of category	Strong	51.3	48.7	5.5	94.5	1.63	833.4 (56.2)
		Weak	47.9	52.1	5.5	94.5	1.55	870.8 (67.1)
2 nd half of session	1 st half of category	Strong	60.3	39.7	6.1	93.9	1.81	821.7 (49.1)
		Weak	50.5	49.5	6.1	93.9	1.56	849.8 (54.0)
	2 nd half of category	Strong	45.8	54.2	4.7	95.3	1.57	835.1 (73.4)
		Weak	41.8	58.2	4.7	95.3	1.47	866.7 (26.1)

2 seconds	Within-category	Relatedness	Hits	Misses	False Alarms	Correct Rejections	d' score	Average RT (SD)
1 st half of session	1 st half of category	Strong	76.4	23.6	7.3	92.7	2.17	1008 (73.3)
		Weak	71.4	28.6	7.3	92.7	2.01	1135 (117.3)
	2 nd half of category	Strong	72.9	27.1	6.5	93.5	2.13	1060 (84.6)
		Weak	72.1	27.9	6.5	93.5	2.10	1155 (117.3)
2 nd half of session	1 st half of category	Strong	74.1	25.9	5.5	94.5	2.24	1015 (106.4)
		Weak	55.4	44.6	5.5	94.5	1.73	1091 (122.4)
	2 nd half of category	Strong	67.9	32.1	4.7	95.3	2.14	1055 (75.6)
		Weak	49.6	50.4	4.7	95.3	1.67	1122 (106.9)

Footnote: Data expressed as percentages of target-present and target-absent trials. Data were divided into the first and second half of each category, allowing within-category fatigue to be assessed. They were also divided into the first and second half of each experimental session, allowing across-category fatigue to be assessed. These data are broken down into the two presentation speeds and strong/weak targets. The distractors are shared and equally distributed 'within' each category; resulting in an equal number of false alarms and correct rejections for the strong/weak targets. RT reported in milliseconds (standard deviations

Table 6.2: Signal detection scores for Experiment 2: Taxonomic-matching.

Across-category	Within-category	Hits	Misses	False Alarms	Correct Rejections	<i>d'</i> score	Average RT (SD)
1st half of session	1st half of category	79.7	20.3	3.1	96.9	2.81	857.5 (29.5)
	2nd half of category	75.2	24.8	3.7	96.3	2.60	850.9 (39.7)
2nd half of session	1st half of category	79.0	21.0	3.2	96.8	2.90	867.5 (27.5)
	2nd half of category	71.9	28.1	3.9	96.1	2.50	865.9 (38.2)

Footnote: Data expressed as percentages of target-present and target-absent trials. Data were divided into the first and second half of each category, allowing within-category fatigue to be assessed. They were also divided into the first and second half of each experimental session, allowing across-category fatigue to be assessed. RT reported in milliseconds (standard deviations).

Table 6.3: Signal detection scores for Experiment 3: Feature-matching.

Across- category	Within-category	Hits	Misses	False Alarms	Correct Rejections	<i>d'</i> score	Average RT (SD)
1 st half of session	1 st half of category	58.94	44.77	7.88	92.12	1.62	887.8 (37.0)
	2 nd half of category	56.70	48.30	7.29	92.71	1.59	892.4 (52.2)
2 nd half of session	1 st half of category	59.17	44.92	7.29	92.71	1.66	874.0 (45.2)
	2 nd half of category	52.16	52.84	7.88	92.12	1.43	878.1 (55.1)

Footnote: Data expressed as percentages of target-present and target-absent trials. Data were divided into the first and second half of each category, allowing within-category fatigue to be assessed. They were also divided into the first and second half of each experimental session, allowing across-category fatigue to be assessed. RT reported in milliseconds (standard deviations).

Table 6.4: Signal detection scores for Experiment 4: Effect across modalities.

Modality	Within-category	Hits	Misses	False Alarms	Correct Rejections	<i>d'</i> score	Average RT (SD)
Pictures	1 st half of category	87.2	12.8	4.5	95.6	3.02	715 (63.5)
	2 nd half of category	85.7	14.3	5.6	94.4	2.97	716 (77.6)
Words	1 st half of category	88.1	11.9	8.8	91.2	2.66	948 (38.1)
	2 nd half of category	87.7	12.3	8.8	91.2	2.65	949 (39.5)
Interleaved Pictures	1 st half of category	86.1	13.9	10.8	89.2	2.30	731 (62.8)
	2 nd half of category	84.3	15.7	15.7	84.3	1.97	700 (69.2)
Interleaved Words	1 st half of category	87.6	12.4	8.4	91.6	2.46	981 (52.1)
	2 nd half of category	87	13	10.4	89.6	2.21	982 (60.1)

Footnote: Data expressed as percentages of target-present and target-absent trials. Data were divided into the first and second half of each category, allowing within-category fatigue to be assessed. They were also divided into the first and second half of each experimental session, allowing across-category fatigue to be assessed, shown individually for the pictures, words and the interleaved (split by pictures and words) modalities. RT reported in milliseconds (standard deviations).

Table 6.5: Signal detection scores for Experiment 5 (Effect of divided attention)

Single condition	Within-category	Hits	Misses	False Alarms	Correct Rejections	<i>d'</i> score	Average RT (SD)
Strong items	1st half of category	77.2	22.8	5.3	94.7	2.64	840 (42.7)
	2nd half of category	71.8	28.2	4.9	95.1	2.49	853 (39.7)
Weak items	1st half of category	44.8	55.2	5.3	94.7	1.67	911 (43.6)
	2nd half of category	39.6	60.4	4.9	95.1	1.56	920 (46.6)
Dual condition	Within-category	Hits	Misses	False Alarms	Correct Rejections	<i>d'</i> score	Average RT (SD)
Strong items	1st half of category	76.8	23.3	5.5	94.5	2.47	852 (43.6)
	2nd half of category	67.1	32.9	5.1	94.9	2.27	865 (41.5)
Weak items	1st half of category	39.5	60.5	5.5	94.5	1.39	919 (48.8)
	2nd half of category	38.4	61.6	5.1	94.9	1.47	924 (48.1)

Footnote: Data expressed as percentages of target-present and target-absent trials. Data were divided into the first and second half of each category, allowing within-category fatigue to be assessed. They were also divided into the first and second half of each experimental session, allowing across-category fatigue to be assessed. These data are broken down into the two conditions (single/dual) and strong/weak targets. The distractors are shared and equally distributed 'within' each category; resulting in an equal number of false alarms and correct rejections for the strong/weak targets. RT reported in milliseconds (standard deviations).

APPENDIX B: Chapter 3 – Semantic control deficits and retrieval-induced changes in categorisation: evidence from ageing and semantic aphasia.

Table 6.6: Summary of significant results from GLM for the age comparisons including data from 24 younger participants, examining the effects of group, relatedness and within-category performance, for the key dependent measures- response sensitivity, response accuracy and response times.

	Older adults vs. Undergraduates		
	Response Sensitivity	Response Accuracy	Response Times
Fixed effects:	Wald χ^2, p	Wald χ^2, p	Wald χ^2, p
Group	16.96, < .001	5.07, .024	$p > .1$
Relatedness	157.21, < .001	100.73, .001	487.18, < .001
Within-category	$p > .1$	3.51, .061	13.48, < .001
Interactions:			
Group x Relatedness	91.04, < .001	$p > .1$	55.92, < .001
Group x Within-category	$p > .1$	$p > .1$	3.57, .059
Group x Relatedness x Within-category	8.92, .003	7.83, .005	$p > .1$

Footnote: Table presents analyses employing (i) mixed effects modelling for response sensitivity (i.e., GLM preserving performance information for each category for each participant and treating participants as a random effect – this allowed RT per category to be included as a covariate of no interest), (ii) mixed effects modelling for response accuracy (i.e., GLM preserving performance information for each category for each participant, and (iii) mixed effects modelling for response times (i.e., GLM preserving performance information for each category for each participant).

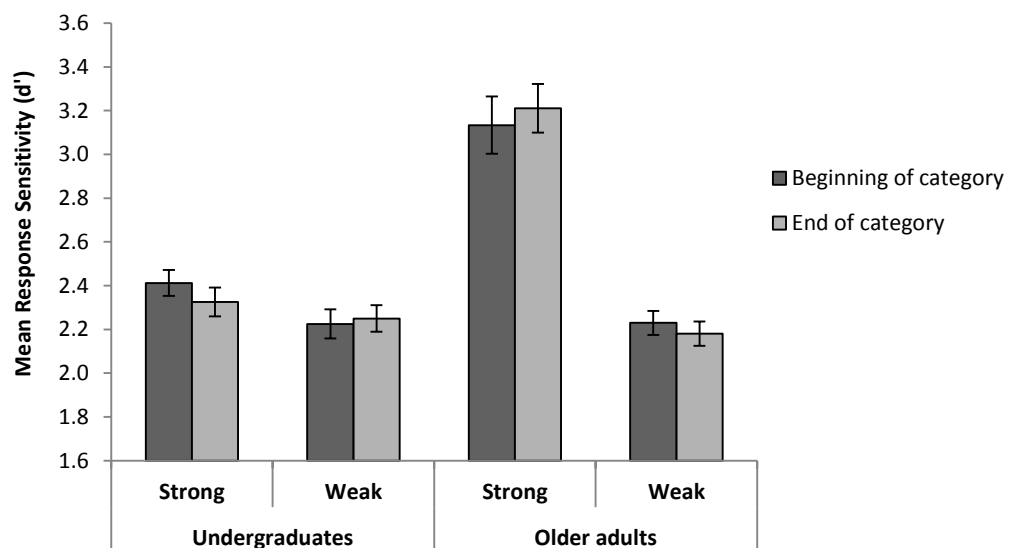


Figure 6.1: Mean response sensitivity (d') for the first and second half of each category (within-category performance), split by strong and weak targets for the two age groups, including data from 24 undergraduate participants. Error bars show SE of the mean.

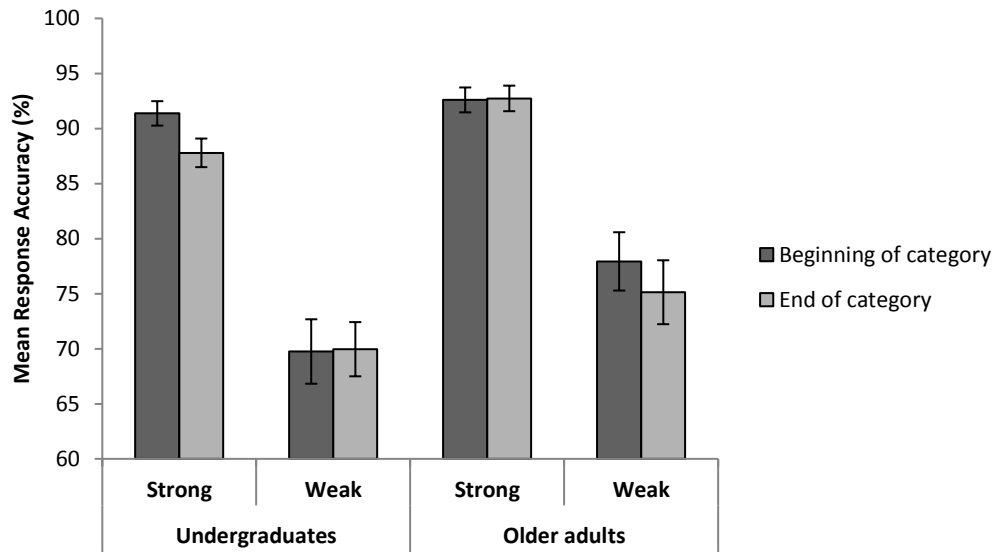


Figure 6.2: Mean response accuracy (%) for the first and second half of each category (within-category performance), split by strong and weak targets for the two age groups, including data from 24 undergraduate participants. Error bars show *SE* of the mean.

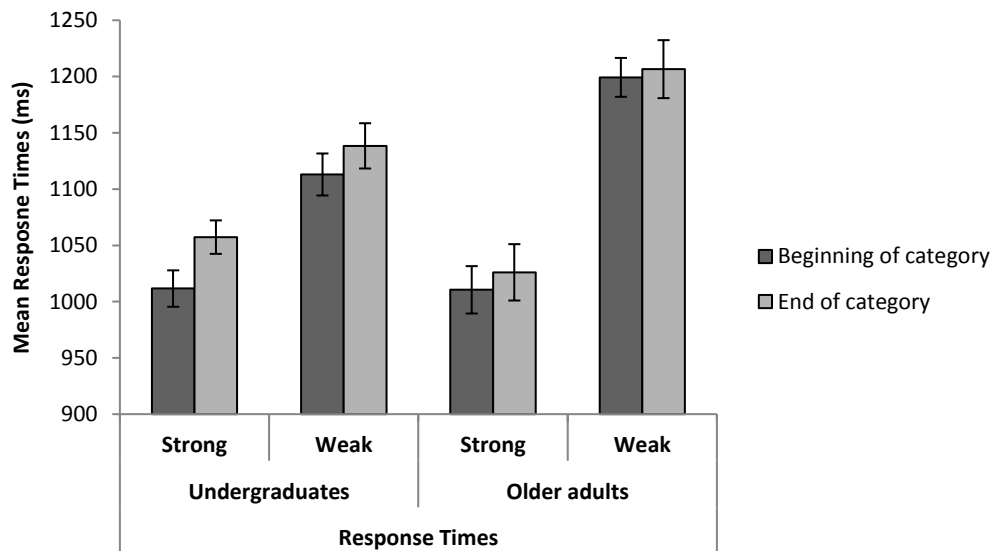


Figure 6.3: Mean response times (ms) for the first and second half of each category (within-category performance), split by strong and weak targets for the two age groups, including data from 24 undergraduate participants. Error bars show *SE* of the mean.

APPENDIX C: Thematic matching (mean lexical frequency (LF) = 19.7, SD = 40.07)

Christmas (LF = 58)		Bedroom (LF = 81)		Bathroom (LF = 87)		Living Room (LF = 94)		Supermarket (LF = 83)		Garden (LF = 50)	
Strong (51)	Weak (65)	Strong (58)	Weak(103)	Strong (63)	Weak (110)	Strong (36)	Weak (151)	Strong (98)	Weak (67)	Strong (36)	Weak (65)
tree	religion	bed	hanger	Bath	tiles	armchair	remote	shop	health	flowers	party
card	bible	chamber	chair	scales	house	bookcase	brick	store	provision	lawn	wall
cake	reindeer	curtains	books	soap	wallpaper	carpet	fire	basket	street	hose	path
pudding	family	carpet	robe	water	brush	cushion	cottage	money	queue	fence	peas
December	star	floor	linen	towel	rack	curtains	door	shelf	carrier	grass	hut
tinsel	manger	pillow	bunk	sink	bedroom	telephone	house	cash	handbag	shed	pest
snow	elves	suite	apartment	toilet	apartment	television	hearth	bargains	container	plant	fete
mistletoe	holiday	sheets	house	shower	roll	sofa	shelter	counter	goods	weeds	butterfly
cracker	stable	clock	desk	tap	cloth	lamp	ceiling	bag	warehouse	shrub	roots
present	queen	slippers	chest	basin	door	magazine	family	food	trade	gate	umbrella
Unrelated (LF = 62)		Unrelated (LF = 70)		Unrelated (LF = 35)		Unrelated (LF = 46)		Unrelated (LF = 42)		Unrelated (LF = 44)	
economics	staff	staff	fish	army	rat	forest	buttons	hospital	drama	ship	dog
doctor	army	news	zoo	uniform	tie	nurse	football	homework	flute	teacher	flute
rugby	ballet	physics	tune	staff	patient	farm	ballet	dentist	subject	drama	injury
bed	forest	tiger	teacher	teacher	exam	zoo	injury	reptiles	history	guitar	reptiles
rat	school	injury	captain	coat	injury	guard	grammar	exam	birds	rugby	piano
dentist	sailor	farm	cat	physics	drama	rugby	clerk	palace	ballet	ambulance	radio
football	university	nurse	grammar	flute	violin	captain	hockey	fur	rat	medicine	cat
captain	typist	sailor	coat	doctor	lion	typist	tie	library	guard	economics	zoo
buttons	cat	exam	football	grammar	guitar	tiger	shirt	clerk	zoo	army	buttons
basin	clerk	forest	economics	economics	nurse	drama	staff	typist	soccer	surgery	news
waiter	physics	army	English	harp	captain	sailor	news	ship	violin	captain	typist
window	cricket	birds	sheep	birds	utensil	post	lion	piano	grammar	instrument	grammar
guard	farm	post	flute	fur	tiger	history	guitar	injury	cat	post	doctor
shower	injury	ballet	gear	reptiles	cook	tune	flute	radio	coat	mouth	ballet
patient	grammar	school	university	hockey	king	economics	dog	king	forest	uniform	harp
dog	nature	drama	subject	cricket	cat	doctor	teacher	ambulance	captain	violin	king
ambulance	ship	guard	elephant	ballet	suit	reptiles	army	buttons	tiger	tune	trousers
sheep	skirt	nature	reptiles	English	forest	uniform	gear	cricket	nature	utensil	gear
uniform	study	history	office	piano	guard	nature	cricket	hockey	physics	fish	patient
zoo	utensil	fur	cricket	instrument	gear	birds	physics	farm	patient	staff	tiles

Farm (LF = 100)		School (LF = 114)		Hospital (LF = 72)		Office (LF = 130)		Kitchen (LF = 105)		Builder (LF = 126)		Police LF = (66)	
Strong (121)	Weak (79)	Strong (121)	Weak (106)	Strong (41)	Weak (104)	Strong (151)	Weak (109)	Strong (117)	Weak (93)	Strong (204)	Weak (48)	Strong (72)	Weak (60)
yard	truck	children	revise	doctor	matron	work	rank	sink	door	house	block	car	gun
stable	stock	uniform	trip	ward	sick	desk	gossip	table	fire	bricks	permission	jail	helmet
plough	harvest	desk	meal	injury	death	secretary	record	food	dinner	stone	trade	crime	beat
field	timber	teacher	room	accident	ache	staff	department	utensil	stool	trowel	master	station	dogs
country	eggs	class	noise	sterile	fracture	file	clerk	saucepan	cabinet	cement	yard	uniform	blue
house	food	bell	milk	pain	care	suit	accounts	larder	bottle	contract	dig	crook	patrol
cow	mud	bus	cap	wound	bone	stationary	money	oven	sweep	site	plan	criminal	trial
tractor	land	exam	tie	illness	baby	typist	trade	bread	store	materials	dump	cop	force
dung	gate	homework	period	nurse	X-ray	firm	union	knife	smoke	work	wire	law	emergency
dogs	manager	pupils	results	ambulance	bed	hours	profit	mother	warm	saw	metals	inspector	file
Unrelated (LF = 79)		Unrelated (LF = 42)		Unrelated (LF = 35)		Unrelated (LF = 30)		Unrelated (LF = 54)		Unrelated (LF = 56)		Unrelated (LF = 50)	
beach	ambulance	manufacur e	cow	sheep	forest	tractor	birds	beach	coast	beach	eggs	fish	dung
sail	firm	reptiles	farm	beach	plough	wound	yard	sheep	football	sail	cow	sick	tiger
desk	tutor	nurse	hospital	sail	sailor	crime	ship	sail	ambulance	desk	nurse	yard	maid
swim	needle	chimney	police	tractor	lion	waves	shell	tractor	island	swim	anchor	tent	picnic
office	army	sail	army	boat	crime	exam	grass	boat	file	gun	sea	shell	beach
clerk	guard	captain	court	grass	ocean	cow	anchor	grass	sailor	class	clerk	mud	homework
class	hockey	sailor	sale	farm	lessons	blood	hat	jail	forest	waves	elephant	anchor	sale
waves	ocean	ambulance	factory	teacher	manufacur e	criminal	tent	teacher	desk	maid	matron	hat	holiday
boat	lion	tiger	plough	jail	sun	chimney	forest	tent	mud	exam	lessons	ship	camp
exam	lessons	waitress	tractor	football	anchor	lion	sail	trade	foam	jail	tutor	forest	dairy
surf	teacher	anchor	horse	tiger	saucepan	injury	nurse	anchor	sweep	doctor	picnic	sail	surf
cop	illness	sheep	ship	coast	elephant	matron	giraffe	police	lessons	reptiles	student	teacher	student
book	yachts	crime	ocean	cow	hockey	saucepan	beach	books	knife	fish	sheep	broom	party
bed	waitress	merchant	patient	captain	chimney	sheep	patient	tiger	contract	holiday	court	ocean	milk
nurse	typist	waves	swim	waitress	bees	larder	hens	surf	dung	camp	patrol	tractor	waitress
staff	matron	blood	boat	surf	mop	swim	ambulance	clerk	figures	surf	illness	cow	island
captain	secretary	dung	coast	factory	guard	mop	stable	bed	warm	police	mop	doctor	hens
carpet	seaweed	elephant	yachts	sale	trade	foam	ocean	bus	typist	sailor	crime	swim	plank
patient	crime	sand	forest	kennel	Clingfilm	bees	hockey	horse	stationary	lion	lettuce	counter	merchant
sailor	uniform	surf	beach	waves	sand	cake	camp	lion	gun	book	ambulance	plough	field

Beach (LF = 52)		Clothes Shop (LF = 121)		Picnic (LF = 70)		Library (LF = 126)		Dentist (LF = 31)		Restaurant (LF = 98)		Birthday Party (LF = 131)	
Strong (59)	Weak (45)	Strong (95)	Weak (144)	Strong (68)	Weak (72)	Strong (156)	Weak (96)	Strong (44)	Weak (17)	Strong (67)	Weak (129)	Strong (193)	Weak (69)
sea	birds	store	factory	field	BBQ	books	table	tooth	glasses	food	owner	cake	age
boat	hat	counter	return	rug	cake	card	coffee	drill	floss	tip	vegetarian	present	dance
seaweed	anchor	town	street	lunch	holiday	novel	service	doctor	tool	menu	chips	card	crisps
sun	tree	wardrobe	goods	grass	friends	work	poems	surgery	mould	meal	sauce	games	greetings
sand	crowd	rail	wrap	sandwiches	lettuce	information	study	filling	decay	chef	party	candles	shop
pebble	chips	money	bag	napkins	rest	reference	magazine	chair	tongue	table	spices	gift	photographs
waves	foam	sale	buttons	Clingfilm	wasp	shelf	notes	injection	ache	bill	utensil	food	voucher
sail	wind	model	discount	sun	basket	author	literature	gum	medicine	waiter	service	friends	candy
swim	holiday	fashion	work	countryside	cook	papers	knowledge	dentures	hygiene	diner	window	money	baby
ball	port	changing rooms	assistant	lunchbox	weather	archive	glasses	mouth	saliva	bistro	money	children	cook
Unrelated (LF = 59)		Unrelated (LF = 54)		Unrelated (LF = 56)		Unrelated (LF = 38)		Unrelated (LF = 49)		Unrelated (LF = 35)		Unrelated (LF = 48)	
office	tie	farm	swim	jail	hospital	football	sauce	harp	shirt	hockey	reptiles	exam	lion
reptiles	library	hospital	teacher	crime	clerk	farm	injury	typist	grammar	sailor	grammar	grammar	gear
class	factory	police	elephant	office	police	tune	mouth	rat	drama	sledge	tune	cricket	birds
nurse	plough	beach	waves	gun	army	nurse	gear	tiger	ship	drama	linen	homework	snow
teacher	uniform	court	law	sheep	sale	fur	zoo	reptiles	uniform	zoo	typist	football	army
chimney	trade	field	typist	typist	factory	dog	ship	tie	rugby	nurse	injury	cat	soccer
gun	lion	cow	exam	library	boarding	cavity	cat	hockey	piano	tiger	teacher	teacher	window
desk	court	army	surf	uniform	plough	fish	piano	fish	ambulance	economics	fur	bed	dentist
file	window	plough	ocean	tiger	tractor	shirt	tie	song	gear	instrument	religion	buttons	ambulance
carpet	patient	tractor	mop	exam	homework	birds	guard	flute	tune	buttons	lion	desk	zoo
staff	criminal	bed	ship	street	trade	rugby	ambulance	school	coat	farm	captain	basin	hockey
cow	matron	nurse	captain	nurse	guard	utensil	trousers	skirt	buttons	tie	reindeer	rat	reptiles
door	sheep	hockey	patient	staff	cop	instrument	hockey	guard	nature	cavity	physics	tiger	university
army	tractor	tiger	jail	chimney	counter	army	buttons	forest	fur	lawn	cat	sailor	clerk
exam	ward	sun	lion	tutor	shelf	sailor	coat	physics	violin	sheep	dog	tiles	injury
sweep	economy	tree	injury	illness	buy	soccer	patient	guitar	zoo	surgery	rugby	carpet	coat
metals	jail	cop	ambulance	mop	sailor	tiger	captain	university	history	gift	nature	nurse	patient
hens	tiger	tutor	forest	anchor	sand	violin	news	soccer	sailor	post	ambulance	doctor	forest
clerk	thieves	horse	lorry	lion	ambulance	suit	diner	cat	football	bed	hammer	farm	economics
suit	saucepan	bees	matron	duty	blood	sheep	screw	teacher	wood	chamber	clerk	history	weapon

APPENDIX D: Taxonomic matching (mean lexical frequency (LF) = 19.7, SD = 40.07)

Kitchen Items (LF = 15)		Vehicles (LF = 35)		Tools (LF = 6)		Furniture (LF = 39)		Vegetables (LF = 6)		Stationary (LF = 10)	
Related		Related		Related		Related		Related		Related	
knife	grater	car	truck	screwdriver	wrench	chair	wardrobe	potato	turnip	paper clip	pencil sharpener
fork	ladle	bus	ferry	tape measure	chisel	dining table	stool	carrot	parsnip	rubber	stapler
teaspoon	sieve	lorry	yacht	hacksaw	drill	desk	mirror	onion	courgette	pen	scissors
saucepan	tongs	bicycle	taxi	Stanley knife	clamp	dresser	sofa	peas	butternut squash	pencil	folder
corkscrew	jug	motorcycle	jeep	hammer	torch	cabinet	bench	beans	pepper	post-it notes	label
frying pan	spatula	tram	helicopter	trowel	ladder	bookcase	cupboard	celery	cucumber	highlighter	ring binder
rolling pin	whisk	tractor	scooter	nails	crowbar	bed	couch	broccoli	lettuce	ruler	notebook
bowl	cup	train	coach	screws	chainsaw	drawers	shelves	cauliflower	mushroom	protractor	marker pen
jar	plate	van	speedboat	pliers	shears	recliner	coffee table	sweet potato	cabbage	compass	plastic wallet
jug	wooden spoon	aeroplane	ship	wire cutters	axe	lamp	armchair	leek	radish	clipboard	drawing pin
Unrelated (LF = 26)		Unrelated (LF = 14)		Unrelated (LF = 14)		Unrelated (LF = 25)		Unrelated (LF = 22)		Unrelated (LF = 15)	
saxophone	notebook	passion fruit	scone	beans	tulip	t-shirt	tangerine	mosquito	screws	raspberry	dress
yacht	eyebrow	accordion	lily	lettuce	broccoli	lemonade	aeroplane	trombone	mirror	lager	coffee
socks	armadillo	church	scorpion	milkshake	skirt	pigeon	cider	lorry	cymbals	parrot	whale
locust	jeans	mango	sofa	library	chicken	jeep	jellyfish	dolphin	cabinet	doughnut	beetle
museum	trumpet	daisy	orange juice	melon	celery	lobster	flapjack	vest	torch	rain coat	falcon
pliers	crow	monkey	apricot	flea	shark	cherry	zebra	lamb	squid	orchid	bun
post office	screwdriver	cardigan	freezer	shrimp	cheesecake	donkey	water	hoover	tiger	canary	courgette
jacket	compass	cake	mockingbird	gorilla	sheep	daffodil	town hall	butterfly	wire cutters	sieve	armchair
wolf	chapel	oyster	whisk	shirt	leopard	pasty	apple	stapler	bookcase	tram	tuna
axe	horse	plate	trousers	muffin	owl	cabbage	scooter	telephone	violin	piano	cockroach
owl	ship	beer	pig	primrose	gin	blackcurrant	lilac	rhinoceros	computer	tumble dryer	stingray
chainsaw	cello	shelves	marigold	mushroom	café	hawk	cattle	hammer	panda	moth	ginger bread
speedboat	chisel	lettuce	clothes shop	eel	bank	helicopter	wasp	mussel	shorts	sunflower	socks
cinema	train	hamster	banana	hoodie	carnation	cinema	radish	cd-player	neck	jellyfish	teaspoon
camel	crocodile	t-shirt	Meerkat	guinea pig	duck	flute	wine	kingfisher	eagle	trowel	theatre
scorpion	police station	croissant	wardrobe	bagel	waffle	pepper	onion	suit	hairdryer	ladle	grapes
vulture	leopard	harp	nightclub	brandy	sunflower	bread	tractor	giraffe	bear	haddock	cupcake
rain coat	earlobe	bowl	guitar	art gallery	sparrow	shorts	clarinet	taxi	dragonfly	television	reindeer
bed	centipede	lion	raspberry	peach	scarf	train station	spider	protractor	lamp	kiwi	poppy
motorcycle	suit	microwave	peacock	crumpet	whiskey	elephant	seahorse	cat	rubber	bench	motorcycle

Musical instruments (LF = 5)		Beverages (LF = 52)		Town centre buildings (LF = 53)		Fruits (LF = 6)		Clothing (LF = 23)		Sea creatures (LF = 4)	
Related		Related		Related		Related		Related		Related	
piano	oboe	water	beer	church	bakery	plum	kiwi	dress	jacket	dolphin	plaice
trumpet	saxophone	orange juice	wine	town hall	nightclub	apricot	blackberry	trousers	rain coat	crab	cod
flute	recorder	coffee	vodka	bank	library	peach	pear	tights	shorts	seahorse	jellyfish
clarinet	accordion	tea	gin	clothes shop	art gallery	raspberry	nectarine	shirt	hoodie	shark	haddock
French horn	drum kit	hot chocolate	whiskey	train station	museum	apple	grapes	tie	cardigan	octopus	lobster
trombone	harp	coke	cocktail	cinema	post office	mango	blackcurrant	skirt	jeans	squid	mussel
bassoon	violin	lemonade	cider	cafe	chapel	strawberry	passion fruit	socks	jumper	eel	shrimp
cymbals	cello	milkshake	port	hotel	theatre	tangerine	melon	t-shirt	scarf	seal	oyster
cornet	xylophone	apple juice	brandy	shopping mall	police station	banana	cherry	cagoule	blouse	tuna	starfish
organ	guitar	lager	sherry	pub	restaurant	orange	pineapple	vest	suit	whale	stingray
Unrelated (LF = 10)		Unrelated (LF = 15)		Unrelated (LF = 10)		Unrelated (LF = 12)		Unrelated (LF = 21)		Unrelated (LF = 26)	
ferry	chimpanzee	paper clip	microwave	spatula	tractor	trousers	iris	cow	highlighter	nightclub	art gallery
orange	sweet pea	recliner	moth	lily	tea	grasshopper	squid	trumpet	nails	desk	rose
jar	seal	van	hoodie	rain coat	shears	spatula	sparrow	orange juice	van	cider	mosquito
cheetah	cricket	plate	clipboard	chisel	tomato	stool	leopard	chimpanzee	bluebell	hotel	robin
couch	oven	plaice	drill	turnip	cider	bassoon	Stanley knife	sieve	telephone	carnation	gorilla
hacksaw	dresser	skirt	tractor	helicopter	shirt	pub	ladybird	parsnip	beetle	jumper	radio
bowl	vodka	pie	French horn	dolphin	mosquito	hot chocolate	shoulder	restaurant	vulture	pasty	cheesecake
brownie	dishwasher	ant	cauliflower	centipede	passion fruit	cheetah	parrot	raspberry	sunflower	blackberry	drawing pin
quail	squid	drawers	lobster	hoover	mussel	aeroplane	louse	waffle	coffee table	whiskey	library
caterpillar	kettle	crowbar	iron	meerkat	vulture	yacht	cardigan	tuna	organ	pepper	strawberry
lavender	thistle	xylophone	bagel	sparrow	ladle	seahorse	spatula	chainsaw	banana	cupboard	plate
shrimp	goose	tape measure	hippopotamus	dining table	recliner	hawk	cornet	ring binder	flapjack	coach	bus
jumper	jeans	crab	tie	tangerine	wardrobe	chicken	axe	tram	bear	theatre	socks
rolling pin	shopping mall	chapel	screwdriver	ship	sherry	toaster	shark	folder	cheek	cherry	oven
post office	pencil	shortbread	cupcake	crab	socks	drum kit	woodpecker	apricot	goat	kettle	ginger bread
strawberry	starfish	forget-me-not	grater	peas	violets	museum	mussel	cheesecake	scorpion	hamster	crowbar
cookie	Swiss roll	bee	lamp	calf	stingray	cup	stereo	marigold	violets	forehead	carrot
marker pen	knee	leg	duck	waffle	notebook	bicycle	accordion	lion	oyster	dragonfly	trombone
leek	scissors	starfish	raven	blouse	peach	hacksaw	screws	tooth	tongs	rubber	coke
ladder	cagoule	hummingbird	tulip	frying pan	pliers	dragonfly	rain coat	scooter	car	clarinet	wasp

Flowers (LF = 9)		Creepy crawlies (LF = 4)		Foreign/Zoo animals (LF = 9)		Birds (LF = 3.8)		Body parts (LF = 39)	
Related		Related		Related		Related		Related	
lily	lavender	ladybird	moth	bear	gorilla	pigeon	woodpecker	ankle	mouth
thistle	lilac	spider	flea	lion	meerkat	owl	kingfisher	chest	lip
carnation	marigold	bee	dragonfly	wolf	panda	eagle	peacock	cheek	tooth
rose	orchid	mosquito	caterpillar	elephant	reindeer	sparrow	hawk	elbow	earlobe
daffodil	sunflower	ant	centipede	giraffe	leopard	crow	canary	fingers	forehead
bluebell	poppy	wasp	cricket	rhinoceros	chimpanzee	parrot	quail	wrist	neck
primrose	sweet pea	beetle	scorpion	hippopotamus	crocodile	robin	hummingbird	knee	shoulder
forget-me-not	daisy	grasshopper	cockroach	tiger	armadillo	vulture	falcon	jaw	toes
iris	tulip	butterfly	louse	fox	monkey	dove	raven	leg	chin
hyacinth	violets	fruit fly	locust	zebra	cheetah	blackbird	mockingbird	arm	eyebrow
Unrelated (LF = 16)		Unrelated (LF = 29)		Unrelated (LF = 17)		Unrelated (LF = 22)		Unrelated (LF = 26)	
pig	Swiss roll	clarinet	coach	hacksaw	jumper	coffee	pasty	kiwi	pineapple
bookcase	lion	lemonade	jug	pencil	scooter	cinema	restaurant	knife	cabbage
ruler	truck	hotel	spatula	grater	cello	mango	cherry	milkshake	chainsaw
coffee	couch	apple	cat	blackberry	bank	drawers	hoover	giraffe	coach
cookie	label	cabinet	croissant	harp	blender	chisel	bagel	brownie	tea
elbow	vodka	broccoli	gorilla	clamp	speedboat	tongs	corkscrew	cabinet	café
fox	desk	scissors	blender	hoodie	rain coat	tie	bakery	plum	orange
shrimp	library	recorder	cocktail	computer	lettuce	dog	piano	wrench	bluebell
hoodie	wolf	cider	teaspoon	bagel	radish	muffin	pub	jeep	dove
drum kit	jacket	cup	van	lily	theatre	radio	oven	hotel	fruit fly
chainsaw	waffle	knee	lettuce	compass	lilac	sofa	pie	flea	dress
spatula	leopard	t-shirt	cymbals	wine	ferry	taxi	telephone	stapler	truck
train station	hammer	parrot	pear	marker pen	accordion	plate	shortbread	donkey	stool
goat	armchair	cow	bed	chapel	armchair	hairdryer	screws	flapjack	violin
leg	helicopter	toaster	dove	passion fruit	cupcake	guitar	ship	panda	bank
dove	brandy	crumpet	tooth	cider	lavender	spider	train	chapel	radio
moth	jellyfish	cucumber	television	whisk	xylophone	beetle	wardrobe	library	parrot
cod	cockroach	shears	sweet pea	muffin	melon	seal	ring binder	iris	daisy
shorts	calf	leek	scarf	heater	bowl	cardigan	whiskey	eagle	haddock
kettle	toes	gin	arm	orchid	pepper	wrench	waffle	scone	beetle

Domestic animals (LF = 24)		Home appliances (LF = 32)		Bakery products (LF = 10)	
Related		Related		Related	
cat	guinea pig	blender	television	muffin	crumpet
dog	duck	toaster	refrigerator	cookie	doughnut
horse	goose	hoover	oven	brownie	Swiss roll
cow	parrot	heater	microwave	croissant	pie
goat	hamster	washing machine	stereo	scone	ginger bread
pig	turkey	kettle	telephone	pastry	waffle
chicken	calf	hairdryer	iron	bread	flapjack
donkey	sheep	computer	radio	bagel	cheesecake
camel	cattle	dishwasher	freezer	bun	cupcake
rabbit	lamb	tumble dryer	cd-player	cake	shortbread
Unrelated (LF = 21)		Unrelated (LF = 11)		Unrelated (LF = 10)	
dining table	parsnip	potato	aeroplane	screwdriver	trowel
onion	lemonade	trousers	rose	crab	meerkat
town hall	strawberry	wolf	crumpet	beetle	peacock
primrose	bread	cocktail	mushroom	giraffe	violin
pie	microwave	carrot	starfish	guitar	wardrobe
jeans	ship	centipede	locust	yacht	leopard
blackberry	suit	kingfisher	cupcake	crow	eagle
recliner	daffodil	shark	vodka	rhinoceros	ankle
beans	refrigerator	goat	rain coat	jellyfish	lorry
whiskey	oboe	bun	carnation	woodpecker	fox
shears	cabbage	sherry	canary	crocodile	tumble dryer
jar	jeep	pineapple	duck	blouse	chimpanzee
telephone	bowl	harp	caterpillar	scooter	falcon
broccoli	nectarine	squid	tiger	camel	rubber
cornet	shortbread	hoodie	suit	jacket	compass
beer	wrench	sunflower	courgette	bank	saxophone
chair	motorcycle	sparrow	pear	paper clip	cinema
ferry	bench	lobster	ginger bread	guinea pig	centipede
muffin	brownie	bagel	reindeer	whale	armadillo
computer	freezer	turnip	oyster	scarf	scorpion

APPENDIX E: Feature matching (mean lexical frequency (LF) = 28.9; SD = 56.8)

Flat (LF = 32)		Strong-smelling (LF = 41)		Green (LF = 10)		Brown (LF = 18)		Heavy (LF = 52)		Black (LF = 10)	
Related		Related		Related		Related		Related		Related	
plate	key	detergent	skunk	emerald	guacamole	acorn	pine cone	gravestone	statue	peppercorns	spider
magazine	paper	soap	garlic	broccoli	lettuce	gravy	bread	bowling ball	tyre	record	liquorice
pancakes	blackboard	nail polish	sewage	jade	spinach	cork	whisky	computer	bed	coal	mascara
coins	CD	landfill	sweat	frog	moss	walnut	cocoa	elephant	piano	leather jacket	soot
towel	comb	socks	sulphur	cactus	grass hopper	bear	cigar	truck	tumble dryer	ravens	crow
TV	mirror	lemons	garbage	runner beans	peas	potato	pretzel	anchor	wardrobe	tar	prunes
iron	laptop	cheese	petrol	kiwi	garden string	bagel	conkers	car	log	gorilla	panther
spatula	rug	sour milk	onions	grass	lime	coconuts	cello	dumbbells	vending machine	ebony	treacle
biscuit	tiles	bread	feet	ivy	pistachio	wood	cardboard	couch	luggage	bat	tyres
coaster	postcard	cigarettes	fish	Christmas tree	caterpillar	cinnamon	chocolate	television	mattress	blackboard	sunglasses
Unrelated (LF = 31)		Unrelated (LF = 24)		Unrelated (LF = 23)		Unrelated (LF = 24)		Unrelated (LF = 22)		Unrelated (LF = 17)	
palm tree	elves	napkins	wall	ginger	ravens	cd	apple	pillow	lighter	jade	peas
eggs	aeroplane	clarinet	saucer	caramel	mustard	emerald	cherry	biscuit	ruler	butter	milk
shower block	strawberry	statue	kettle	bone	London bus	mango	wedding dress	cling film	towel	apple	sea gull
hose	blender	wrench	brush	horse	marshmallows	roses	candy floss	cushion	whistle	broccoli	moss
onion	waves	poster	blanket	cranberries	snow	water	zebra	paper	tin foil	egg	lettuce
dumbbell	cucumber	glass	map	ebony	sheep	clouds	lettuce	pencil	trainers	coriander	olive oil
paint	nuts	handbag	desk	cherry	stop sign	mayonnaise	postman's van	needle	mug	ivy	rice
conditioner	apple	pillow	butterfly	butter	lobster	glass	nectarine	lollipop	wafer	runner beans	meringue
bird cage	bridge	ladder	mattress	coffee	raspberries	whipped cream	London bus	balloon	wire	bone	marshmallows
milkshake	tree	necklace	scissors	lipstick	meringue	Santa	tongue	stamp	crepe	caramel	pistachio
plant	sweet jar	scales	bicycle	eggs	post-box	needle	whale	grass	t-shirt	foam	mango
car	moon	guitar	watch	bat	milk	milk	tomato	silk	salad	blood	lawn
earth	bulb	pen	tissue box	crows	record	checkered flag	peas	plate	tray	emerald	pineapple
panda	cow	tray	CD	coal	mascara	carrots	lime	feather	ticket	chalk	kiwi
basin	open fire	spatula	camera	flour	chips	polar bears	soccer ball	gas	key	flour	salt
wasp	bucket	chair	umbrella	rodent	sea gull	leprechaun	oranges	shorts	sheets	cheese	lime
tulip	sun	lipstick	envelope	foam	salt	grapes	sweetcorn	thread	bowl	chef hat	oranges
glue	bees	tap	photograph	blood	ruby	bone	panda	postcard	debit card	cherry	mustard
sofa	glass	nuts	flour	blackboard	panda	shamrock	penguin	bread	skewer	frog	polar bear
cone	ear phones	pencil	trophy	chocolate	cow	radiator	snow	butterfly	umbrella	grass	candy floss

Rough (LF = 13)		Hot (LF = 24)		Runny (LF = 62)		Sticky (LF = 9)		Cold (LF = 12)		Soft (LF = 22)	
Related		Related		Related		Related		Related		Related	
Christmas tree	crocodile	porridge	oven	milk	custard	cello tape	mango	beer	air conditioner	flowers	tie
door mat	wood chippings	stove	fireplace	sweat	shampoo	glue	cement	glaciers	Antarctica	marshmallows	sandwiches
rose bush	charcoal	radiator	iron	water	honey	dough	lollipops	freezer	grapes	mattress	feather
sandpaper	tyre	lava	toaster	coffee	petrol	caramel	paste	polar bears	popsicle	scarf	grass
tree bark	sand	sun	hair straightener	wine	glue	honey	syrup	ice cream	yogurt	dough	slippers
hay	mesh	chilli pepper	coals	blood	olive oil	jelly	sweets	snow	skating rink	robe	rug
brush	rope	candle	BBQ	gravy	milkshake	spiders web	treacle	salad	sleet	scone	towel
gravel	potpourri	kettle	furnace	paint	perfume	candy floss	paint	Pluto	snowman	cushion	linen
bricks	coconut	engine	heater	tea	ketchup	duct tape	slug	icicles	fridge	bread	blanket
basket	beard	light bulbs	Jacuzzi	beer	treacle	stamps	blue tack	igloo	milkshake	cake	hamsters
Unrelated (LF = 23)		Unrelated (LF = 11)		Unrelated (LF = 30)		Unrelated (LF = 37)		Unrelated (LF = 39)		Unrelated (LF = 29)	
Clingfilm	piano	pudding	banana	guitar	poles	briefcase	horse	computer	chef hat	wall	boat
beer	milkshake	apple	cucumber	photographs	wasp	cash machine	hair brush	stamp	coal	Frisbee	desk
coffee	shampoo	mattress	ice cream	sunglasses	peanuts	box	guitar	car	bone	cage	chimney
glue	silk	post-box	salt	bill	diary	aeroplane	mattress	paper	cigarette	barrel	pegs
cushion	linen	flower pot	pencil	walkie talkie	mannequin	bench	mug	wedding dress	feather	statue	tablets
grass	milk	yogurt	holly	brick	record	bicycle	ladder	light bulbs	sunglasses	trophy	scissors
blood	mattress	magazine	cupcake	box	bottle	basket	magazine	ball	steam	lorry	fossils
cd	olive oil	feather	cherry	Clingfilm	wheel	book	laptop	iron	olive oil	rake	fridge
feather	scarf	snowman	pineapple	napkins	skipping rope	airbag	fridge	Jacuzzi	tin foil	bicycle	coins
bread	petals	shopping trolley	refrigerator	glass window	stone	camera	kettle	engine	plug	tray	computer
aubergine	perfume	sugar	petals	scissors	rug	car	petals	rug	kettle	flower pot	dumbbell
hamsters	petrol	bicycle	body lotion	timber	wrench	boots	feather	bees	mascara	lectern	chairs
honey	paint	acorn	Clingfilm	rake	drums	caravan	Antarctica	toaster	butterfly	blackboard	building
custard	mirror	leaf	rake	television	novel	cloth	napkins	saucepan	television	bone	shell
dough	scone	chalk	scissors	bunting	hanger	bus	lettuce	books	lava	wrench	van
cake	sandwiches	beer	violin	piano	wood chippings	chair	curtains	firewood	umbrella	injection	bricks
flowers	photographs	microphone	rubber	saucepan	stick	bottle	computer	coffee	hair brush	tap	fence
postcard	robe	nectarine	apron	door	cracker	blender	frame	chalk	hairdryer	bucket	ladder
ketchup	marshmallows	juice	brush	light bulb	laptop	carpet	necklace	eggs	photographs	bowl	television
gravy	rug	coins	banana	manuscripts	hair net	bridge	coins	sun	tongue	stairs	train

Shiny (LF = 41)		Smooth (LF = 22)		Slippery (LF = 26)		Black & White (LF = 15)		Noisy (LF = 16)		Round (LF = 25)	
Related		Related		Related		Related		Related		Related	
saxophone	lighter	glass	petals	detergent	satin	chequered flag	Oreo	horn	gong	satellite dish	peas
spanner	mirror	computer screen	spoons	gel	oil	killer whale	newspaper	vacuum cleaner	dogs	tyre	cookie
cufflinks	kitchen foil	diamond	grapes	noodles	silk	panda	dominos	fireworks	microphone	apple	plate
gold ring	eyes	hummus	body lotion	icicle	ice cubes	football	pirate flag	snoring	babies	clock	doughnut
sink	motorbike	postcard	ice rink	rink	butter	penguin	Dalmatian	aeroplane	drums	marbles	coin
nail clippers	sunglasses	key	leaf	frog	lotion	crosswords	skunk	guns	stereo	ladybird	Frisbee
coins	sequins	cream cheese	aubergine	slug	soap	cow	referee shirt	alarms	lawnmowers	globe	ring
puddle	spoon	feather	apple	snake	fish	Guinness	zebra	racing car	thunder	wheel	button
fire	bulb	pebble	silk	bath tub	banana peel	piano	dice	speakers	whistle	eye	football
chandelier	keys	coins	CD	bouncy castle	grease	checkerboard	barcode	washing machine	lion	CD	saucer
Unrelated (LF = 28)		Unrelated (LF = 12)		Unrelated (LF = 20)		Unrelated (LF = 27)		Unrelated (LF = 24)		Unrelated (LF = 23)	
daisy	timber	sandpaper	fibre sponge	clippers	brush	grass	apple	ketchup	cheese	stable	lock
newspaper	peanuts	porcupine	wood chippings	fibre sponge	basket	Santa	petals	lipstick	needle	toothbrush	cleaver
letter	towel	alligator	potpourri	barbed wire	tablets	honey	cherry	binoculars	books	speakers	boat
eye shadow	tea bag	razor	rose bush	gloves	butterfly	coins	peanuts	giraffe	plug	stairs	knife
horse	crow	hair rollers	clippers	fossils	pillow	mirror	wasp	napkins	rope	sofa	display board
curtains	paper	Frisbee	ginger	sandpaper	cactus	peas	tree	salt	blanket	socks	gloves
forest	pillow	net	fence	armadillo	roof tiles	kiwi	sandwiches	daffodil	cherry	tissue box	carrier bags
manuscripts	weeds	doormat	Velcro	Velcro	desk	foam	gas	towel	soap	pew	bus
blanket	shorts	grater	hay	hair brush	building	tomato	tongue	spoon	spinach	towel	cheque
blueberries	receipt	mesh	bricks	napkins	crocodile	wine	wood chippings	apron	pudding	post-box	books
monkey	panda	sand	coconut	bread	paper	lava	sun	pencil	bed	oven	label
flour	tiger	pine cone	tree bark	cow	ring	Clingfilm	lion	raspberries	thread	tongs	bread
cow	tablets	scratching post	building	shorts	biscuit	globe	forest	windows	teabag	shorts	dogs
elephant	smoke	toast	Christmas tree	wood chippings	hairdryer	lipstick	lager	grass	gloves	wallet	camera
coffee beans	soil	barbed wire	crocodile	cupcake	tooth	custard	weeds	rubber	mug	wardrobe	hutch
mattress	throws	dry skin	hedgehog	sugar cubes	bone	tangerine	shark	ice cream	postcard	podium	computer
cloth	socks	roof tiles	rocks	sea gull	skewer	lettuce	leprechaun	petals	pie	rucksack	grass
bread	sheets	armadillo	cactus	mesh	toaster	cigarette	mango	caramel	onion	seatbelt	comb
lion	sand	rope	beard	rust	microphone	ladybird	blood	mustard	bowl	ticket	apron
blusher	sandwiches	firewood	brush	ice cubes	bricks	teeth	chips	flour	charcoal	lighter	robe

Square/Rectangle (LF = 69)		Red (LF = 20)		Hard (LF = 47)		White (LF = 36)	
Related		Related		Related		Related	
postcard	toaster	roses	tongue	clothes pegs	statue	snow	tooth
envelope	ice cubes	ketchup	strawberries	barrel	shell	salt	sea gull
books	blackboard	cherry	blood	nails	fossils	chalk	swan
door	mattress	phone box	lipstick	stone	pebble	meringue	rice
stamp	shopping trolley	ruby	Santa	saucepan	door	flour	bone
bed	placemat	holly	tomato	helmet	hammer	sugar	lard
dice	television	Ferrari	London bus	plank	chopping board	chef hat	wedding dress
passport	laptop	postman's van	post-box	tooth	table	paper	milk
chopping board	tissue box	stop sign	poppy	brick	sculpture	marshmallows	envelope
brick	briefcase	lobster	fire engine	blackboard	bone	foam	sheep
Unrelated (LF = 11)		Unrelated (LF = 27)		Unrelated (LF = 23)		Unrelated (LF = 34)	
shark	macaroni	trolley	coffee	sofa	fuel	crisps	wasp
ice cream cone	stocking	sugar	gold	shampoo	linen	bees	post box
ramekin	tyre	mosquitoes	ladder	socks	chef hat	blood	sun
doughnut	sausage	spider web	lion	paint	gloves	chips	lion
exercise ball	blueberries	wire	sea gull	oil	baking paper	fire	wooden stick
barrel	tie	silver foil	cockroach	syrup	cloth	gold	holly
scissors	wheel	rake	mirror	pillows	beer	bricks	ketchup
bone	wellies	pool	moon	shorts	flowers	cherry	timber
skipping rope	roses	stable	bread	towel	cake	biscuit	tongue
horse	cello tape	receipt	Clingfilm	napkins	doughnut	blackboard	lifeguard
pebbles	vegetables	spanner	milk	sauce	cupcake	firewood	tree
lettuce	tinsel	tongs	lettuce	scone	flour	forest	pepper
screws	globe	wasp	cement	milk	exercise ball	barrel	tractor
crab	hazelnuts	sea	crisps	sandwiches	curtain	coffee	seatbelt
saucepan	umbrella	snow	fossils	pudding	carpet	bonfire	oil
holly	bubbles	panda	charcoal	rug	chips	grass	sea
slippers	trowel	pond	chips	tinsel	apron	dung	wood chippings
chandelier	star	piano	ice cubes	tea	ice cream	broom	mosquitoes
cow	tomato	peas	bone	tongue	butterfly	cockroach	woodlouse
peas	candy floss	grass	weeds	mattress	tie	charcoal	weeds

APPENDIX F: Thematic matching – Across modalities (mean lexical frequency (LF) = 57.7, SD = 112)

Airport (LF = 49)		Café (LF = 31)		Clothes shop (LF = 108)		Football match (LF = 31)		Hospital (LF = 68)		Hotel (LF = 62)	
Strong (33)	Weak (65)	Strong (31)	Weak (31)	Strong (82)	Weak (134)	Strong (36)	Weak (25)	Strong (62)	Weak (73)	Strong (99)	Weak (26)
terminal	lift	scone	sofa	money	return	player	t-shirt	illness	care	holiday	toothbrush
passport	stairs	coffee	syrup	bag	discount	team	advertisement	doctor	fracture	double bed	cafe
flight	restaurant	tea	candle	store	factory	stadium	water bottle	bed	isolation	room service	lounge
customs	belt	coffee maker	receipt	model	town	goal post	alcohol	ambulance	death	reception	trolley
suitcase	officer	spoon	meeting	assistant	rail	yellow card	lights	X-ray	sick	luggage	window
check-in	hall	cake	display counter	sale	goods	scarf	gloves	patient	mask	room	Jacuzzi
aeroplane	alcohol	snack	apron	mannequin	work	score board	boots	sterile	baby	receptionist	shampoo
runway	perfume	menu	card machine	mirror	counter	referee	pub	accident	matron	tourist	curtains
security	control	waiter	tip	fashion	wardrobe	ball	refreshments	ward	crèche	En-suite	kettle
luggage	notice board	biscuit	wallet	changing rooms	buttons	pitch	stairs	injury	bone	bed	sofa
Unrelated (LF = 27)		Unrelated (LF = 42)		Unrelated (LF = 42)		Unrelated (LF = 34)		Unrelated (LF = 62)		Unrelated (LF = 23)	
trophy	slippers	chamber	tape measure	weeds	sink	wall paper	caravan	postcard	house	sale	tongue
sweep	director	cemetery	stopwatch	saucepan	lettuce	curtains	briefcase	ham	ship	bees	patrol
teacher	homework	bone	tractor	envelope	pillow	coffee	fashion	trainers	bouncer	Frisbee	track
field	red card	carpet	oxygen mask	coach	tank	hair net	salt	manuscripts	baking paper	leaflet	eggs
cake	collars	bed	referee	clippers	tablets	ocean	rock pool	mud	chimney	chalk	officer
saucepan	club	hens	exhibits	tray	pier	throws	litter tray	grass	beer	glass screen	display board
candles	tip	cage	nurse	beach	card	smoke	diary	sand	hymn	perfume	chopping board
vegetarian	tyre pump	wardrobe	model	motorway	milk jug	dinner	carrier	pulpit	beach	basket	VIP box
fan	sermon	research	blockage	fish	skipping rope	basket	student	diesel	advertisement	warehouse	seatbelt
chef	steak	December	den	food	bin	blanket	engineer	palm tree	bonfire	customs	ear protection

Living room (LF = 85)		Petrol station (LF = 215)		Railway station (LF = 38)		Shed (LF = 20)		Bathroom (LF = 66)		Chocolate factory (LF = 20)	
Strong (105)	Weak (66)	Strong (119)	Weak (310)	Strong (27)	Weak (49)	Strong (27)	Weak (14)	Strong (75)	Weak (58)	Strong (28)	Weak (11)
carpet	brick	fuel	bin	track	policemen	screws	cupboard	toilet	cloth	consumer	pipe
ceiling	remote	petrol pump	chocolate	train	newspaper	padlock	firewood	tap	rack	machine	chemicals
armchair	hearth	motorway	can	ticket	bench	paint tin	clippers	shower	door	hair net	overalls
cushion	bookcase	cars	fire	display board	shop	garden	BBQ	water	bedroom	plastic mould	gloves
curtains	cottage	tanker	toilet	conductor	yellow line	toolbox	woodlouse	bath	brush	wrapper	canteen
lamp	door	diesel	pricelist	briefcase	holiday	lawnmower	chairs	basin	cologne	worker	lorry
house	extension	shop	magazine	steam	bag	spade	bulb	towel	scales	manufacture	fridge
sofa	magazine	money	flowers	luggage	stairs	ladder	spider web	sink	apartment	conveyor belt	wage
television	fire	cash machine	coffee shop	clock	automatic doors	tools	bucket	tiles	pipes	box	warehouse
family	telephone	tyre pump	loyalty card	waiting room	engineer	hose	drawer	soap	plumber	shop	building
Unrelated (LF = 46)		Unrelated (LF = 67)		Unrelated (LF = 58)		Unrelated (LF = 96)		Unrelated (LF = 52)		Unrelated (LF = 35)	
trip	nurse	ship	flip-flops	hanger	membership card	pub	sun	stationary	microphone	aeroplane	tie
coffee shop	trowel	cruise	organ	cloth	waves	ambulance	food	debit card	cross	book	fracture
manager	car	groceries	jail	mould	grill	gossip	blood	bell	remote	injection	dentures
hose	flip-flops	sand	camp	mixer	table	chef	literature	photographs	safety goggles	stadium	traffic
swimmer	classroom	armchair	woodlouse	plastic mould	bible	Clingfilm	sofa	meal	torch	resort	maid
statue	drivers licence	cement	apron	sand	cleaning equipment	post-box	money	guitar	flag	conductor	elephant
yellow card	holiday	stairs	bench	music	scratching post	goalkeeper	barmaid	bread	cookie	runway	houses
cheque	padlock	tiger	house	sail	bed	milk	class	menu	wage	swimsuit	cement
Shower	sick	student	baby	menu	pen knife	van	card	saw	gum	straightener	sweat
hairdryer	lighter	flour	panda	mop	stage	archive	oxygen mask	shop	chips	bell	drums

Driving (LF = 65)		Hairdressers (LF = 55)		Birthday party (LF = 141)		Lecture hall (LF = 47)		Pet shop (LF = 41)		Police (LF = 61)	
Strong (32)	Weak (98)	Strong (37)	Weak (72)	Strong (77)	Weak (205)	Strong (52)	Weak (43)	Strong (61)	Weak (20)	Strong (68)	Weak (55)
motorway	light	curler	money	games	crisps	projector	table	birds	bell	jail	hat
indicator	tank	salon	shower head	Food	Cook	student	row	cage	collars	criminal	dogs
wheel	wash	comb	mop	Friends	Money	screen	file	bowl	tablets	car	court
driver	radio	shampoo	radio	candles	Voucher	pen	water bottle	cat	treats	helmet	statistics
gear	air conditioning	straightener	wedding	Photographs	Baby	lecturer	speakers	hutch	toys	emergency	defence
license	go-cart	hair	spray	balloon	dance	information	pointer	fish	brush	constable	file
pedal	window	mirror	stool	Card	children	handouts	podium	hamsters	nuts	uniform	desk
traffic	bridge	scissors	tea	Cake	suit	blackboard	laptop	wood chippings	leads	patrol	lights
brakes	clamp	hairdryer	silver foil	Present	Candy	books	computer	food	shampoo	crime	duty
fuel	crossing	brush	magazine	hat	roast	exam	doodle	aquarium	litter tray	station	collar
Unrelated (LF = 45)		Unrelated (LF = 54)		Unrelated (LF = 82)		Unrelated (LF = 53)		Unrelated (LF = 53)		Unrelated (LF = 57)	
dairy	island	wristband	beat	preview	toothbrush	bills	roll	law	chairs	oil	BBQ
birds	spray	drill	eggs	path	water bottle	wash	scales	open fire	cash machine	row	curtains
dinner	piano	crab	baptism	trolley	rake	goods	wallpaper	glasses	captain	stairs	cattle
stairs	manager	ball	water bottle	razor	Shop	ticket	whistle	archaeology	throws	remote control	cat
wasp	table	gate	fossils	luggage	sink	money	cutter	pillar	truck	field	Candy
oyster	cake	projector	fete	Umbrella	Religion	soap	hut	phone	holiday	lunch	seaweed
union	homework	aircraft	mosquitos	octopus	Clock	loin	oven	timetable	painting	poster	Author
canteen	hat	hearth	party	Fence	work	countryside	bus	Christmas cards	trees	pain	art
label	plan	sandwiches	cupcake	vending machine	toilet	island	sand	Jacuzzi	ice cubes	porter	milk
aquarium	charcoal	garden	water fountain	period	window	tracks	dog	pipes	weight	snow	steam

The sea (LF = 38)		Zoo (LF = 90)		Supermarket (LF = 97)		Restaurant (LF = 92)		Foreign Holiday (LF = 51)		Museum (LF = 45)	
Strong (48)	Weak (28)	Strong (110)	Weak (71)	Strong (60)	Weak (134)	Strong (80)	Weak (103)	Strong (47)	Weak (39)	Strong (37)	Weak (53)
holiday	camera	giraffe	leaflet	trolley	container	meal	utensil	Hotel	cockroach	archaeology	ticket
lifeguard	island	elephant	playground	food	counter	waiter	chips	cruise	flag	statue	research
coast	rock pool	keeper	turn style	shelf	mother	menu	cloth	passport	First aid kit	exhibits	animals
surfboard	treasure	children	map	basket	carrier	food	money	beach	ski	fossils	pamphlet
ocean	salt	monkey	school	car park	handbag	chef	carpet	suitcase	Life jacket	sculpture	map
waves	towel	panda	field	goods	flowers	tip	vegetarian	photos	mosquitos	painting	extinct
shore	pier	tiger	uniform	cash	family	bill	spices	camera	museum	exhibition	archive
beach	octopus	cage	den	bargains	bag	bistro	suit	sun	postcard	guide	shop
swimsuit	lighthouse	tourist	camera	shop	money	table	party	abroad	book	gallery	security guard
fish	port	souvenirs	glass window	store	warehouse	diner	window	sunglasses	snow	art	students
Unrelated (LF = 53)		Unrelated (LF = 29)		Unrelated (LF = 33)		Unrelated (LF = 27)		Unrelated (LF = 58)		Unrelated (LF = 84)	
doctor	sachets	plumber	indicator	tinsel	dancer	gallery	muscles	chair	utensil	bell	ladder
treadmill	belt	pebble	pulpit	choir	sick	wound	Decay	sausages	knowledge	runway	country
comb	slicer	hotel	cake	souvenir	pupils	Novel	stamp	sofa	death	pudding	manger
money	carriage	altar	cabinet	holiday	illness	newspaper	Lawn	helmet	cracker	food	jukebox
fashion	recipe	kitchen	hearth	sailor	suitcase	military	shampoo	Spider web	stool	meal	sand
sauce	dung	bicycle	holly	gate	vault	tractor	mud	class	mistletoe	festival	speaker
cigarette	glow stick	Clingfilm	chair	cross-trainer	friends	aisle	Medicine	revise	scone	gun	screen
knife	postman	laptop	dumbbell	sofa	forest	stable	clamp	Silver foil	instructor	countryside	pebble
receipt	prayer	candles	cigarette	cement	passport	ache	valve	laptop	Football match	towel	tree
clock	darts	exam	bible	hike	apartment	nurse	trimmer	party	dumbbell	clerk	hose

Kitchen (LF = 121)		Bank (LF = 68)		Gym (LF = 39)		Dentist (LF = 27)		Camping (LF = 42)		Bakery (LF = 37)	
Strong (85)	Weak (157)	Strong (78)	Weak (59)	Strong (31)	Weak (48)	Strong (25)	Weak (30)	Strong (47)	Weak (36)	Strong (25)	Weak (49)
bread	slice	queue	gold	treadmill	t-shirt	mouth	ache	fire	repellent	cookie	mixer
oven	party	cheque	card	personal trainer	television	surgery	chair	sleeping bag	marshmallows	baker	knife
larder	parlour	safe	branch	cross-trainer	Pilates	filling	saliva	grass	Frisbee	pastry	coffee
stool	door	statement	glass screen	weight	shorts	dentures	tongue	trees	pegs	roll	recipe
dinner	smoke	money	notes	workout	fan	tooth	decay	tent	rope	bun	spices
maid	waiter	manager	vault	exercise mat	music	injection	medicine	caravan	pen knife	bread	tongs
sink	farm	counter	robbery	trainers	ear phones	gum	mould	torch	shower block	oven	menu
food	mother	coins	office	sweat	mirror	floss	glasses	rucksack	cool box	pie	staff
table	bottle	balance	pen	sport	sauna	hygiene	tool	hike	lighter	cake	tray
cabinet	sweep	ATM	clerk	muscles	socks	drill	doctor	forest	friends	dough	chef hat
Unrelated (LF = 40)		Unrelated (LF = 64)		Unrelated (LF = 27)		Unrelated (LF = 36)		Unrelated (LF = 56)		Unrelated (67)	
branch	life jacket	camera	garden	restaurant	butterfly	carving	yard	spotlight	bulb	treasure	airbag
car	policemen	dogs	chocolate	timeline	hutch	leads	passenger	hair	sweep	ATM	t-shirt
doodle	sprinklers	wrap	yard	station	peas	footpath	holiday	stationary	counter	wire	bell
computer	locker	concert	bible	post-box	bowl	discount	security guard	return	factory	scenery	party
stationary	gear	mirror	school	stable	fuel	Street	truck	tap	sofa	bikini	postcard
anchor	pointer	diner	monkey	criminal	milkshake	lion	Handbag	overalls	information	pamphlet	chapel
dance	letter	fire	lunchbox	display counter	lawn mower	sport	exhibition	control	doctor	sports TV	accounts
mud	Reindeer	printer	bucket	candle	double bed	substitute	luggage	ladder	curtains	stop	dump
card	shower	pictures	coast	handouts	boat	breakfast	cottage	turn style	military	land	plunger
dung	sun	check-in	waiter	decoration	camera	coffee maker	pond	oven	fan	pool	tanker

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