An individual differences approach to semantic cognition: Divergent effects of age on representation, retrieval and selection

Paul HOFFMAN

Centre for Cognitive Ageing and Cognitive Epidemiology (CCACE), Department of Psychology, University of Edinburgh, UK

Correspondence to:
Dr. Paul Hoffman
Centre for Cognitive Ageing and Cognitive Epidemiology,
Department of Psychology, University of Edinburgh,
7 George Square, Edinburgh, EH8 9JZ, UK
Tel: +44 (0) 131 650 4654
Email: p.hoffman@ed.ac.uk

Acknowledgements

The work was undertaken by The University of Edinburgh Centre for Cognitive Ageing and Cognitive Epidemiology, part of the cross council Lifelong Health and Wellbeing Initiative (MR/K026992/1). Funding from the Biotechnology and Biological Sciences Research Council (BBSRC) and Medical Research Council (MRC) is gratefully acknowledged. I am grateful to Ellen Fearnley, Emily Hardy, Wing Yee Ho, Eszter Kalapos, Jasmine Kulay, Khushboo Mehra and Adam Ryde for assistance with data collection and to Beth Jefferies for sharing experimental stimuli.

Abstract

Semantic cognition refers to our ability to use acquired knowledge to make sense of the environment and to guide behaviour. This requires representation of knowledge as well as control processes which ensure that currently-relevant aspects of this knowledge are retrieved and selected in any given situation. These abilities can be impaired selectively following brain damage; however, the relationship between them in healthy individuals is not known. In addition, it is commonly assumed that semantic cognition is preserved in later life, because older people have greater reserves of knowledge. However, this claim overlooks the possibility of decline in semantic control processes, which has not been investigated. The study addressed these issues by assessing verbal semantic cognition in 100 young and older adults. Despite having a broader base of semantic knowledge (i.e., wider vocabulary), older people showed specific impairments in semantic control, performing more poorly than young people when required to select among competing semantic representations. Conversely, they showed improved controlled retrieval of less salient information from the semantic store. Within each age group, breadth of semantic knowledge was positively correlated with controlled retrieval but was unrelated to semantic selection ability, which was instead correlated with non-semantic executive function. These findings indicate that three distinct elements contribute to semantic cognition: (a) a store of representations which accumulates throughout the lifespan, (b) processes for controlled retrieval of less salient information from this store, which are also more developed in later life and (c) domain-general executive selection mechanisms that decline in old age. These results provide a new framework for interpreting patterns of spared and impaired verbal abilities in old age.

Introduction

Semantic knowledge, of the meanings of words and properties of objects, shapes our understanding of the world and guides our behaviour. Each of us has a wide range of conceptual knowledge distilled from a lifetime of experiences. Effective semantic cognition – that is, the ability to use semantic knowledge to complete cognitive tasks – requires us to both *represent* this information in an accessible form and to *control* how we access and manipulate it in specific situations (Badre & Wagner, 2002; Hoffman, 2016; Jefferies, 2013; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Yee & Thompson-Schill, 2016). Long-term semantic representation is essential because it allows us to generalise knowledge gained from previous experience into novel situations (Lambon Ralph & Patterson, 2008). If we have a stored representation of the typical characteristics of, for example, a particular breed of dog, when we meet a new member of that breed we can predict its likely behaviour. Cognitive control over the activation and selection of semantic information is also critical because we store a wide range of information about any particular concept and different aspects of this knowledge are relevant in different circumstances (Hoffman, Lambon Ralph, & Rogers, 2013; Saffran, 2000; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). When playing a piano, for example, the functions of the keys and pedals are of central importance. But if one is asked to move the piano across the room, this dominant knowledge is not relevant and must be ignored in favour of focusing on the size, weight and value of the instrument.

There is substantial evidence that the *representation* and *control* elements of semantic cognition are supported by different neural networks and can be independently impaired as a consequence of brain damage (Hoffman, Binney, & Lambon Ralph, 2015; Jefferies & Lambon Ralph, 2006; Warrington & Cipolotti, 1996; Whitney, Jefferies, & Kircher, 2011). Little is known, however, about the relationships between these abilities in the healthy population. Do people who know more have better control of their knowledge, or is the quantity of semantic knowledge an individual possesses independent of their ability to regulate this information? Is cognitive control over semantic information strongly correlated with executive control ability in other domains? And do semantic representation and control decline in parallel as a function of healthy ageing? The present study was designed to investigate these questions.

Evidence from multiple methodologies indicates that semantic representation and control rely on distinct (but interacting) brain regions. The anterior temporal cortices act as a store of conceptual representations, through interaction with modality-specific association

regions (Guo et al., 2013; Hoffman et al., 2017; Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015; Patterson, Nestor, & Rogers, 2007; Pobric, Jefferies, & Lambon Ralph, 2007). Damage to this region results in a profound loss of semantic knowledge, as seen in the neuropsychological syndrome of semantic dementia (Mion et al., 2010; Patterson et al., 2007). In contrast, the controlled use of semantic knowledge is associated with activation in a network of prefrontal, posterior temporal and parietal regions (Noonan, Jefferies, Visser, & Lambon Ralph, 2013; Rodd, Davis, & Johnsrude, 2005; Thompson-Schill et al., 1997). Damage to these regions following left-hemisphere stroke results in impaired ability to inhibit irrelevant semantic information, to retrieve weak or less automatic semantic associations and to understand ambiguous words with competing meanings (Hoffman, Rogers, & Lambon Ralph, 2011; Jefferies & Lambon Ralph, 2006; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010).

The brain regions activated by tasks with high semantic control demands overlap partially with those implicated in the "multiple demand" network, which respond to increased control demands across many cognitive domains (Duncan, 2010; Fedorenko, Duncan, & Kanwisher, 2013). This suggests that processes involved in control of semantic knowledge may overlap with those involved in executive control in other domains. In fact, fMRI studies suggest that semantic control can be fractionated into semantic-specific and domain-general components, which activate neighbouring areas of left inferior prefrontal cortex (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Nagel, Schumacher, Goebel, & D'Esposito, 2008). The first of these is a <u>controlled retrieval</u> mechanism that is engaged when automatic activation of semantic knowledge is insufficient to complete a given task. For example, a participant completing a semantic association task might be asked whether *bee* is associated with *flower* or *tree*. In this situation, automatic processing of the cue may result in activation of the strongest associates of bees (*honey*, *hive* etc.) but fail to activate either of the available response options. Under these circumstances, individuals are assumed to engage in a goal-directed controlled search through the semantic store for the relevant information (Badre & Wagner, 2007). This controlled retrieval process appears to be specific to semantic knowledge. In functional neuroimaging studies, increased need for controlled retrieval is associated with increased activation in the anterior, ventral portion of left inferior prefrontal cortex (BA47) (Badre et al., 2005; Dobbins & Wagner, 2005; Gold et al., 2006; Krieger-Redwood, Teige, Davey, Hymers, & Jefferies, 2015). Structural and functional connectivity studies indicate that BA47 is strongly connected with the anterior temporal regions that code

semantic representations, supporting the view that it is linked specifically with the regulation of semantic knowledge (Jackson, Hoffman, Pobric, & Lambon Ralph, 2016; Jung, Cloutman, Binney, & Ralph, 2016; Von Der Heide, Skipper, Klobusicky, & Olson, 2013).

The second mechanism, here termed semantic selection, is engaged when automatic activation of semantic knowledge results in competition between multiple competing representations, which must be resolved. This is commonly assessed using the feature association task, in which participants are required to match concepts based on specific shared properties (Thompson-Schill et al., 1997). For example, a participant might be asked whether a *wasp* or a *hive* is the same size as a *bee*. In this case, both response options are semantically associated with the cue and they compete with one another for selection. Top-down selection processes are thought to resolve the competition, based on the requirements of the current task (Badre & Wagner, 2007; Kan & Thompson-Schill, 2004). This may involve inhibition of pre-existing but irrelevant semantic links (e.g., *bee-hive*). Of course, the need to select from competing responses is not specific to semantic processing and is a major element of tests of inhibitory executive function like the Stroop task (Cohen, Dunbar, & McClelland, 1990). Increased selection demands in semantic tasks are associated with activation in the posterior portion of left inferior prefrontal cortex (BA44/45) (Badre et al., 2005; Gold et al., 2006; Thompson-Schill et al., 1997). This area is also activated by conditions of high competition in working memory tasks (Badre & Wagner, 2005), the Stroop task (January, Trueswell, & Thompson-Schill, 2009) and other inhibitory tasks (Hazeltine, Bunge, Scanlon, & Gabrieli, 2003) and it shows strong structural connectivity with the domain-general multiple demand network (Jung et al., 2016). These findings suggest that semantic selection may be served by a domain-general executive selection system.

To summarise, neuropsychological and neuroimaging studies indicate a double dissociation between representations of semantic knowledge and the processes that control how this knowledge is used. Semantic control processes also appear to be multidimensional, consisting of semantic-specific processes supporting controlled retrieval of information from memory as well as domain-general selection mechanisms. However, the relationship between these abilities in the healthy population is not clear. Put simply, if you know a lot, are you better or worse at regulating how you access and use this knowledge? Three different potential answers to this question are suggested by three different literatures. First, as the evidence from neuroimaging and neuropsychology suggests, the quantity of knowledge one has and the ability to use it in a controlled fashion may be largely independent of one another.

Alternatively, decades of intelligence research suggests that much individual variation across a wide range of cognitive tasks can be attributed a single general factor (g) (Deary, Penke, & Johnson, 2010; Gottfredson, 1997; Salthouse, 2004). Applied to the semantic domain, this would imply a positive relationship between representation and control: individuals with high general ability should perform well on tests of both. Finally, findings in the episodic memory literature raise the possibility of a negative relationship between quantity of semantic knowledge and ability to control access to this information. In episodic memory studies, when participants learn to associate a large set of information with one particular stimulus, they find it harder to retrieve any particular piece of information from the set (the fan effect; Anderson, 1974; Anderson & Reder, 1999). Extended to the semantic domain, this effect could suggest that individuals with a richer store of knowledge experience greater interference between competing representations and therefore are less efficient at exercising control.

The relationship between semantic control and executive control in other cognitive domains is also unresolved. As discussed earlier, some researchers have suggested that can be fractionated into domain-general and semantic-specific components. However, no studies have directly contrasted semantic control ability with non-semantic tests of executive function in healthy individuals. Such comparisons have been conducted in semantically-impaired stroke patients, who show a positive correlation between semantic control ability and performance on tests of non-semantic executive function (Allen, Martin, & Martin, 2012; Jefferies & Lambon Ralph, 2006). These findings could be taken as evidence that controlled processing of semantic information shares executive resources with other cognitive domains. However, as stroke patients typically have large lesions that span multiple frontal and parietal sites, it may simply reflect greater impairment in multiple, independent systems in patients with larger lesions. The present study provides a new perspective on this debate by assessing the relationship between semantic control and general executive ability in healthy individuals for the first time.

The final issue addressed in this study is the effect of healthy ageing on semantic abilities. It is typically the case that scores on semantic tests remain relatively stable across adulthood, in contrast to the marked declines seen in many other cognitive abilities (Grady, 2012; Nilsson, 2003; Nyberg, Bäckman, Erngrund, Olofsson, & Nilsson, 1996; Park et al., 2002; Rönnlund, Nyberg, Bäckman, & Nilsson, 2005; Salthouse, 2004; Verhaeghen, 2003). Most large-scale studies of cognitive aging have employed vocabulary tests as their primary measure of semantic ability. Meta-analysis indicates that older adults (over 60 years) actually score substantially higher on such tests than young adults (below 30 years; Verhaeghen, 2003). Such

differences are typically explained in terms of older participants continuing to add to the semantic knowledge store throughout their lives. Indeed, greater time spent in formal education appears to account for much of the age effect (Verhaeghen, 2003). Vocabulary tests, which typically probe knowledge of low frequency words, provide a good indication of the breadth and richness of an individual's semantic knowledge store. However, they are not designed to probe executively demanding aspects of semantic processing, such as controlled retrieval of concepts or competition resolution. As a consequence, the effect of ageing on semantic control abilities has not been assessed. This is important because it is possible that this aspect of semantic processing suffers a different fate to that seen for vocabulary measures. Some forms of executive function, outside the semantic domain, deteriorate as people grow older (Hasher & Zacks, 1988; Salthouse & Miles, 2002; Treitz, Heyder, & Daum, 2007; Verhaeghen & Cerella, 2002). It is therefore possible that controlled use of semantic information shows age-related decline, particularly if this shares neural resources with other executive functions. Such declines may be evident even if the amount of knowledge in the semantic system increases.

The present study was designed to investigate differences in semantic abilities in young and older adults, as well as relationships between semantic knowledge, semantic control and non-semantic executive function in each age group. This was achieved by administering tests that probed the size of the semantic knowledge store (i.e., measures of vocabulary size) as well as tests that placed greater demands on controlled use of semantic knowledge (controlled retrieval and semantic selection). We assessed controlled semantic retrieval and semantic selection with separate tests, since these two elements of semantic control appear to dissociate neurally. Of course, these elements of semantic cognition are highly interactive and we assumed that all semantic tasks require each of them to some degree. Thus, none of the tests were expected to index a single element exclusively but they were designed to place greater demands on one element or another. We expected to replicate the established finding that older people have larger and richer repositories of semantic knowledge. However, it was predicted that performance on tests of semantic control would decline in old age.

Method

Participants: Fifty young adults, aged between 18 and 30, were recruited from the undergraduate Psychology course at the University of Edinburgh and participated in the study in exchange for course credit. Fifty older adults, aged between 61 and 91, were recruited from the Psychology department's volunteer panel. A wide range of ages across later life were sampled, to allow for investigation of age effects within the older group as well as comparisons between young and older people. All participants reported to be in good health with no history of neurological or psychiatric illness. Demographic information for each group is shown in Table 2. Young and older adults did not differ significantly in years of education completed ($t(98) = 0.49$, $p = 0.63$).

General cognitive assessments: Participants completed a series of tests of general cognitive function and executive ability. The Mini-Mental State Examination was used as a general cognitive screen. All participants scored 25/30 or above. Task-switching ability was assessed using the Trail-making task (Reitan, 1992). Executive function was also assessed with the Eriksen flanker task (Eriksen, 1995). Participants were presented with a row of five letters and pressed a key to indicate whether the central letter was a H or an N. They were instructed to ignore the four flanking letters on either side of the central target. On Congruent trials, the flanking letters matched the target (e.g., HHHHH) while on Incongruent trials they were inconsistent (e.g., NNHNN). The Incongruent trials therefore required participants to resolve competition between the two possible response options. As a test of complex executive function, a subset of participants (27 young; 26 older) completed a computerised version of the Wisconsin Card-Sorting Test, consisting of 64 trials (Mueller & Piper, 2014). Finally, three categories of verbal fluency were administered, in which participants were given one minute to produce as many words as possible that fit a specific criterion. The criteria included two semantic categories (animals and household objects) and one letter of the alphabet (words beginning with F). Verbal fluency tasks require access to verbal-semantic knowledge but are also assumed to place high demand on executive function.

Tests of semantic control: Participants completed a task that probed two forms of semantic control, using the same design as Badre et al. (2005). The experiment consisted of 8 blocks of 12 trials. In four blocks, participants were asked to make semantic decisions based on global

semantic association. Participants were presented with a probe word and asked to select its semantic associate from either two or four alternatives. The associate was either strongly associated with the probe (e.g., *town-city*) or more weakly associated (e.g., *iron-ring*; see Figure 1). The 24 weak association trials were hypothesised to place greater demands on controlled retrieval of semantic information, because automatic spreading of activation in the semantic network would not be sufficient to identify the correct response (Badre & Wagner, 2007). Psycholinguistic properties of the words used in each condition are presented in Table 1. Words used in the strong and weak association conditions did not differ in mean frequency, concreteness or age of acquisition (all $p > 0.48$). Latent semantic analysis (Landauer & Dumais, 1997) was used to provide an estimate of the semantic relatedness of the probe-target pairs in each condition. As expected, they were significantly more related in the strong association condition ($t(46) = 3.01$, $p = 0.004$). The relationship between probes and foils was assessed in the same way; these were close to zero on average in both conditions, confirming that the foils were semantically unrelated to the probes. This indicates that the foils in this task did not act as strong semantic competitors.

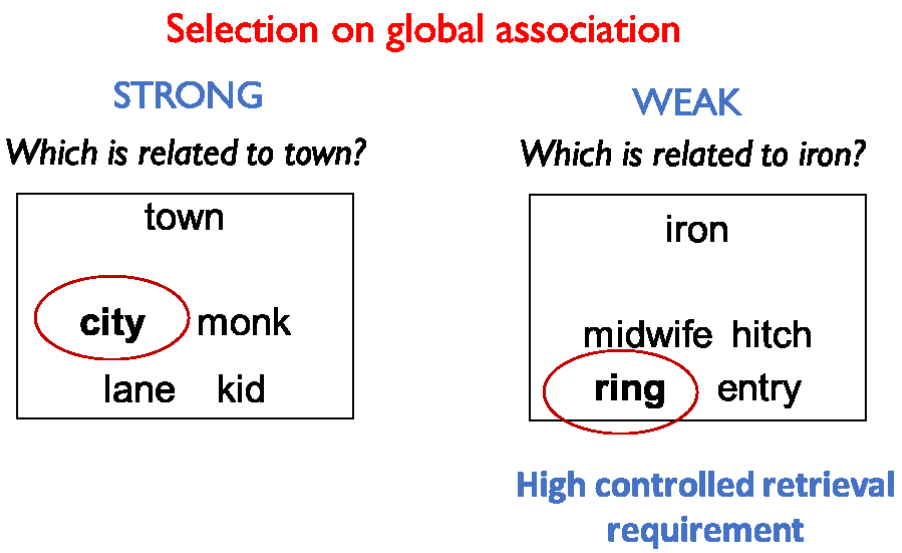

Figure 1: Example trials from global association blocks *The correct response is highlighted in each case.*

Table 1: Mean psycholinguistic properties of words used in semantic tasks

	Strong Global	Weak Global	Cong Feature	Incon Feature	Lex Dec	Synonyms
Frequency (Zipf)	4.23	4.27	4.28	4.22	2.49	2.88
	(0.72)	(0.81)	(0.57)	(0.65)	(0.93)	(1.14)
Concreteness	4.40	4.32	4.68	4.66	3.76	2.59
	(0.76)	(0.73)	(0.45)	(0.41)	(0.92)	(0.83)
Age of acquisition	6.17	6.30	5.97	6.17	11.97	10.89
	(2.42)	(2.12)	(2.29)	(1.99)	(2.68)	(2.97)
Probe-target semantic relatedness	0.40	0.20	0.54	0.00	-	-
	(0.26)	(0.20)	(0.25)	(0.08)		
Probe-foil semantic relatedness	0.01	0.02	0.02	0.23	-	-
	(0.09)	(0.06)	(0.07)	(0.29)		

Standard deviations are shown in parentheses. Word frequencies (on the log-tranformed Zipf scale) were obtained from the SUBTLEX-UK database (Van Heuven, Mandera, Keuleers, & Brysbaert, 2014). Concreteness values were obtained from Brysbaert et al. (2014) and age of acquisition values from Kuperman et al. (2012). Semantic relatedness values were computed using latent semantic analysis (see text for details). Cong = congruent; Incon = incongruent; Lex Dec = lexical decision.

In the other four blocks, participants were asked to select items that matched on particular features (either Colour or Size). This task places high demands on semantic control because participants must direct attention away from global semantic associations and instead attend to specific item properties (Thompson-Schill et al., 1997). At the beginning of each block, participants were given a feature to attend to (e.g., Colour). On each trial, they were provided with a probe and were asked to select, from two or four alternatives, the item that was most similar on the specified feature. There were 24 congruent trials, in which the probe and target shared a pre-existing semantic relationship, in addition to matching on the currently relevant feature (e.g., *cloud-snow*; see Figure 2). On these trials, the foils did not match on the specified feature, nor did they share a global semantic association with the target. These trials therefore placed minimal demands on semantic selection mechanisms because the correct option was the one with the strongest pre-existing relationship with the probe. In contrast, on the 24 incongruent trials the probe and target shared no meaningful relationship, other than matching on the specified feature (e.g., *salt-dove*). Furthermore, one of the foils *did* have

a strong semantic relationship with the probe, although it did not match on the currently relevant feature (*salt-pepper*). These trials placed high demands on selection mechanisms for two reasons: first, because there was no pre-existing semantic relationship between probe and target and second, because the strong but irrelevant relationship between the probe and foil had to be ignored. The properties of the words in each condition are shown in Table 1. Words used in the congruent and incongruent conditions did not differ in mean frequency, concreteness or age of acquisition (all $p > 0.49$). The semantic relatedness of probe and target was stronger in the congruent condition ($t(45) = 9.85$, $p < 0.001$). The relationship between probes and foils was significantly stronger in the incongruent condition ($t(94) = 5.00$, $p < 0.001$), reflecting the fact that a semantically related foil was present in this condition.

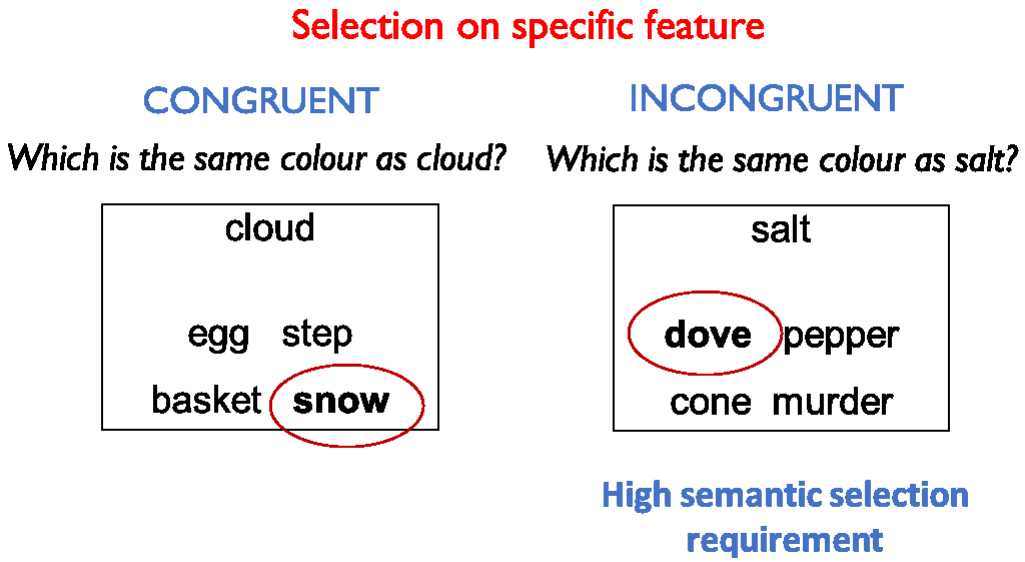

Figure 2: Example trials from feature association blocks *The correct response is highlighted in each case.*

Tests of breadth of semantic knowledge: Participants completed two tasks designed to probe the size of their store of semantic representations. These tasks probed knowledge of the meanings and identities of unusual words that were expected to be unknown to some members of the population. They therefore indexed the breadth of semantic knowledge available to each individual. The first task (Lexical Decision) was the Spot-the-Word Test from the Speed and Capacity of Language Processing battery (Baddeley, Emslie, & Smith, 1992). This was a lexical decision test comprising 60 pairs of letter strings (see Figure 3). On each trial, participants were presented with a real word and a nonword and were asked to select the

real word. Nonwords were phonologically and orthographically plausible, encouraging participants to rely on semantic knowledge for decision-making. The second task (Synonyms) was based on the Mill Hill vocabulary test (Raven, Raven, & Court, 1989), a multiple-choice test in which participants are asked to select the synonyms of particular words. There are two parallel forms of the test. To increase the difficulty of the task, the hardest 22 trials from each parallel form were combined to make a new 44-item test. The test was presented in a four-alternative choice format (see Figure 3).

To ensure that they placed greater demands on the semantic knowledge store, the words used in the semantic knowledge tests were significantly lower in frequency ($t(662) = 20.7$, $p < 0.001$) and concreteness ($t(573) = 25.8$, $p < 0.001$) and were later acquired ($t(615) = 90.0$, $p < 0.001$) than those used in the tests of semantic control (see Table 1).

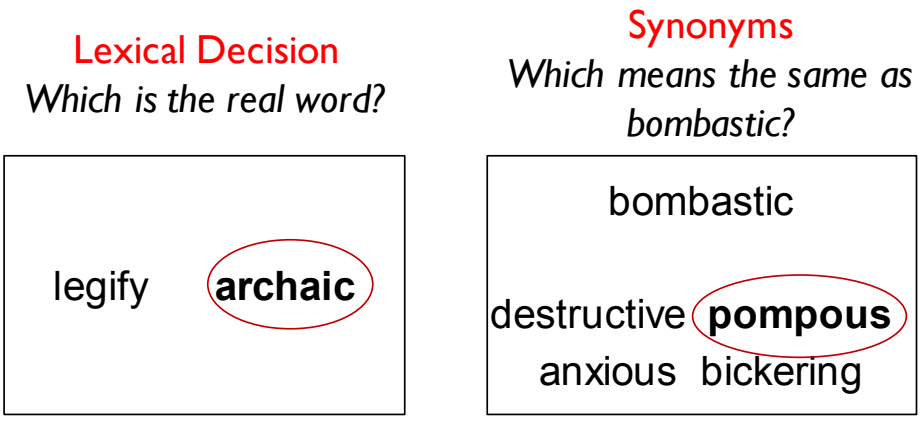

Figure 3: Example trials from the semantic knowledge tests The correct response is highlighted in each case.

Procedure: Participants completed the general cognitive assessments followed by the semantic tasks. Semantic tasks were presented on a PC running Eprime 2.0 software. Participants first completed the Lexical Decision and Synonym tasks and then the semantic control experiment. Each task was preceded by a series of practice trials. Accuracy and reaction times (RTs) were recorded. Participants were instructed to respond as quickly as possible while avoiding mistakes. They were encouraged to guess if unsure of the correct response.

Statistical analyses: Performance measures were computed for each participant on each semantic task by averaging across all trials. Prior to averaging, RTs were screened for outliers

by winsorising any RTs more two standard deviations from a participant's conditional mean (3.6% of trials). At the group level, the influence of outlying data was limited by winsorising any individual scores that fell more than three standard deviations from the group mean. RTs were log-transformed prior to analysis to reduce skew.

To compare effects of semantic control demands in young and older people, results of the semantic control experiment were analysed in a 2 x 2 x 2 ANOVA model that included group as a between-subjects factor and task (global vs. feature judgments) and control demands (high vs. low) as within-subject factors. The weak association condition of the global judgements and the incongruent feature condition were considered to have high control demands. To investigate the two forms of semantic control independently, the two tasks were also analysed separately in 2 x 2 ANOVAs (control x group). Effects of age group on the individual conditions of the semantic control tasks and on the semantic knowledge tasks were assessed using t-tests. To control for multiple comparisons, a Holm-Bonferroni correction was applied to these results (Holm, 1979). Parametric effects of age within the older group were also assessed for the semantic control experiment, using ANCOVA that included age as a continuous covariate.

To investigate the relationships between tests, Pearson's correlations were computed within each age group separately. Test scores were also entered into principal components analysis, in which factors with eigenvalues greater than one were extracted and varimax rotated. These analyses were performed on accuracy data only, as RTs were likely to covary due to variations in general processing speed that were not specific to a particular cognitive domain. Scores on low control semantic conditions and on the Trails and Erikson flanker tasks were not included in these analyses due to ceiling effects.

Results

General cognitive assessments

As shown in Table 2, young and older adults did not differ in MMSE scores. The category and letter fluency tasks showed opposing effects of age, with young adults outperforming their older counterparts for the semantic categories while older people were significantly more successful at producing words beginning with F (although, within the older group, scores on both tasks were negatively correlated with age). Older people produced significantly fewer correct responses and completed fewer categories in the Wisconsin card-

sorting task. Completion times for the Trails task were analysed in a Part x Group ANOVA. Older adults were significantly slower overall ($F(1,98) = 34.0$, $p < 0.001$) and there was a significant interaction between part and group ($F(1,98) = 22.9$, $p < 0.001$), indicating that older adults showed greater slowing on Part B. This part has a greater executive demand because it requires switching between letters and numbers. RTs for the Eriksen flanker task were analysed using Condition x Group ANOVA. The older group were substantially slower ($F(1,98) = 50.9$, $p < 0.001$) but there was no interaction with condition ($F(1,98) = 3.16$, $p = 0.08$). Reaction times, but not accuracies, were correlated with age in the older group.

Table 2: Demographic information and mean test scores for young and older participants

	Young adults	Older adults	Age *r* in older group
N	50	50	
Age	19.1 (1.8)	77.5 (8.6)***	
Sex M:F	13:37	23:27	
Years of education	13.8 (0.9)	14.0 (3.1)	0.11
MMSE /30	28.8 (0.9)	29.0 (1.2)	-0.28*
Wisconsin card-sorting task (% correct)	79.4 (9.3)	56.2 (18.1)***	-0.10
Wisconsin card-sorting task (categories)	3.9 (1.2)	1.7 (1.4)***	-0.26
Category fluency (items per category)	24.6 (5.3)	21.6 (5.0)**	-0.34*
Letter fluency (items per category)	13.8 (4.8)	16.1 (6.5)*	-0.30*
Trails A errors	0.1 (0.2)	0.1 (0.3)	0.04
Trails B errors	0.4 (0.8)	0.7 (1.1)	0.37**
Trails A time (s)	27.8 (9.7)	36.7 (11.7)***	0.64***
Trails B time (s)	46.8 (13.5)	74.6 (31.3)***	0.55***
Eriksen flanker task – Congruent trials accuracy	0.98 (.02)	0.99 (.02)	-0.24
Eriksen flanker task – Incongruent trials accuracy	0.96 (.04)	0.98 (.03)**	-0.11
Eriksen flanker task – Congruent trials RT (ms)	578 (101)	866 (263)***	0.33*
Eriksen flanker task – Incongruent trials RT (ms)	640 (106)	898 (252)***	0.35*

*Standard deviations are shown in parentheses. Asterisks indicate the significance of t-tests comparing young and older adults (Older adults column) and the Pearson's correlation between test scores and age within the older group (r column). * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

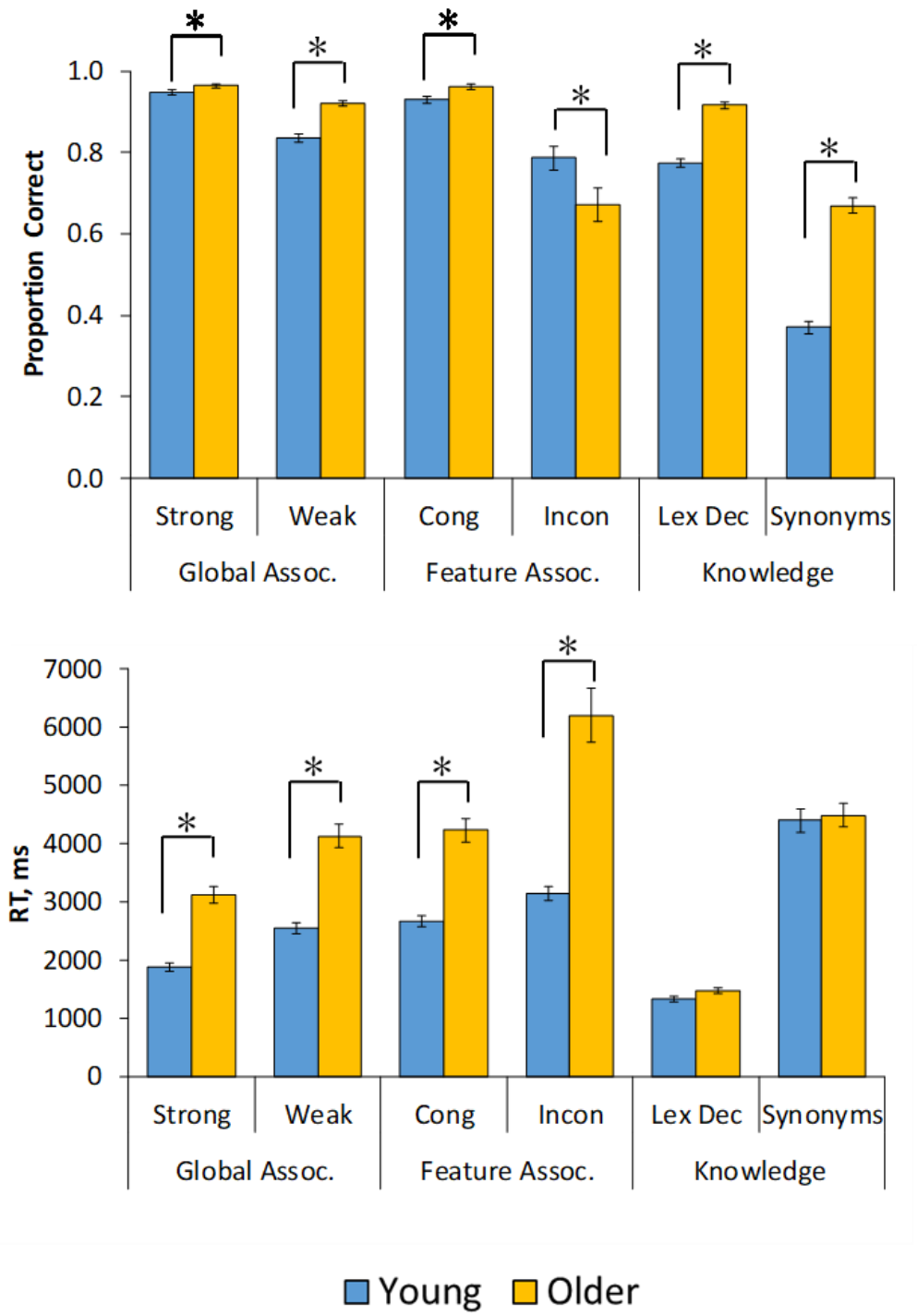

Figure 4: Performance on semantic tests Asterisks indicate significant age differences (Holm-Bonferroni-corrected p < 0.05). Cong = congruent; Incon = incongruent; Lex Dec = lexical decision.

Effects of age on semantic representation and control

Performance on the semantic control tasks are shown in Figure 4. These data were subjected to 2 x 2 x 2 ANOVA that included group as a between-subjects factor and task

(global vs. feature judgments) and control demands (high vs. low) as within-subject factors (where the weak associations and incongruent feature judgements were assumed to have high control demands). The ANOVA results for accuracies and RT are shown in Table 3. Overall, older people were slower to respond but no less accurate. As expected, the feature association task was more difficult than the global association task, with this effect being more pronounced in the older group. The manipulations of control demand also had strong effects on accuracy and RT. Importantly, however, there were highly significant three-way interactions between these factors, suggesting that age had different effects on the two control manipulations.

Table 3: Analysis of semantic control experiment in young and older people

Effect	Accuracy		RT	
	F	*p*	*F*	*p*
Group	0.1	.76	83.8	<.001
Task	42.1	<.001	614.8	<.001
Task x Group	13.9	<.001	5.3	.024
Control	131.5	<.001	479.5	<.001
Control x Group	2.3	.13	11.2	.001
Task x Control	31.1	<.001	1.2	.27
Task x Control x Group	18.2	<.001	22.5	<.001

Degrees of freedom for all tests = 1,98.

The nature of the interaction was investigated with separate 2 x 2 (control x group) analyses for each task. In the global association task, there was a control x group interaction for accuracy ($F(1,98) = 22.2$, $p < 0.001$) as well as a main effect of group ($F(1,98) = 41.6$, $p < 0.001$). As shown in Figure 4, older people produced more correct responses than young people, particularly in the weak association (high control) condition. Older people were generally slower than the young ($F(1,98) = 76.4$, $p < 0.001$), but this effect did not interact with control demand ($F(1,98) = 0.68$, $p = 0.41$). The picture was markedly different for the feature association task. On this task, there was no overall difference in accuracy between young and older people ($F(1,98) = 2.67$, $p = 0.11$). There was, however, a control x group interaction ($F(1,98) = 8.98$, $p = 0.003$) because the older group performed particularly poorly on the incongruent (high control) judgements relative to the young. Indeed, the incongruent feature judgements were the only condition in which older people made more errors than the young (see Figure 4). Analysis of reaction times indicated the older people were slower

overall ($F(1,98) = 83.1$, $p < 0.001$) and that there was again a control x group interaction ($F(1,98) = 22.5$, $p < 0.001$) because they were particularly slow in the incongruent condition.

The picture that emerges from these results is that different forms of semantic control are affected differently by ageing. On the feature association task, older people demonstrated difficulty with semantic selection, when required to inhibit strong but irrelevant associations. In contrast, on the global association task the older group were more able to detect weak associations between concepts, indicating superior controlled retrieval ability. To investigate whether these effects varied with age within the older group, further analyses were performed in this group only, using ANCOVA which included age as a continuous covariate (see Table 4). Accuracy and RT tended to decline as a function of age. Importantly, within the accuracy data there was a control x age interaction and a three-way interaction between task, control and age. Inspection of correlation coefficients indicated that this effect was driven by a negative association between age and performance that was only present on the incongruent trials of the feature association task ($r(48) = -0.32$, $p = 0.024$). Thus, within the older group there was a specific age-related decline in the ability to select task-relevant semantic relationships while ignoring irrelevant associations. No such interactions were observed for RT.

Table 4: Analysis of effects of age within the older group for the semantic control experiment

Effect	Accuracy		RT	
	F	*p*	*F*	*p*
Age	5.19	.027	40.7	<.001
Task	41.0	<.001	393.1	<.001
Task x Age	3.85	.056	1.06	.31
Control	67.3	<.001	243.8	<.001
Control x Age	5.77	.020	2.22	.14
Task x Control	42.6	<.001	5.64	.022
Task x Control x Age	5.59	.022	0.77	.39

Degrees of freedom for all tests = 1,48.

Performance on the two tests probing breadth of semantic knowledge is also shown in Figure 4. Older people performed much more accurately than young people on both of these tasks. There were no group effects on RT, which is surprising, given that the older group were significantly slower across a range of other tasks. Thus, the accuracy and RT data both indicate that older people had a substantial processing advantage on these tasks, indicating that they had a larger and richer store of semantic representations available to them.

Table 5: Correlation matrix for task performance in older group

	1.	2.	3.	4.	5.	6.	7.	8.
1. Lexical Decision	-							
2. Synonyms	.82***	-						
3. Weak Associations	.29*	.36*	-					
4. Incongruent Features	.35*	.19	.16	-				
5. Category fluency	.20	.22	.35*	.26	-			
6. Letter fluency	.03	.14	.40**	.15	.40**	-		
7. Wisconsin card-sorting	.05	-.11	-.09	.15	-.01	-.38	-	
8. Age	.05	.13	-.12	-.32*	-.34*	-.34*	-.10	-
9. Education	.39**	.42**	.15	.08	-.20	.03	-.09	.11

*N = 50 except for correlations involving Wisconsin card-sorting, where N = 26. * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

Table 6: Correlation matrix for task performance in young group

	1.	2.	3.	4.	5.	6.
1. Lexical Decision	-					
2. Synonyms	.64***	-				
3. Weak Associations	.62***	.29*	-			
4. Incongruent Features	.13	.13	.16	-		
5. Category fluency	.07	.13	.13	-.03	-	
6. Letter fluency	.20	.10	.17	.12	.38**	-
7. Wisconsin card-sorting	.11	.16	.03	.43*	.20	.05

*N = 50 except for correlations involving Wisconsin card-sorting, where N = 27. * = p < 0.05; ** = p < 0.01; *** = p < 0.001. Age and Education are not included for the young participants, as the range in these variables was too restricted to give valid results.*

Relationships among semantic and executive tests

A correlation matrix for test scores in the older group is presented in Table 5. Scores on the two semantic knowledge tests were strongly correlated, indicating that both indexed the breadth of participants' semantic knowledge. Both of these tests were positively correlated with years of education. In contrast, there were no correlation between the two tests of semantic control, suggesting that these tapped distinct abilities. However, both semantic control tasks showed weak positive correlations with one or both of the representation tests, indicating a tendency for individuals with more developed semantic representations to be better at exercising control. Performance on the incongruent feature condition and on the two verbal fluency tasks was negatively correlated with age.

To explore the underlying commonalities among tests in more detail, a principal components analysis was performed. There were three factors with eigenvalues greater than one, which together accounted for 73% of the variance in scores (see Table 7). The lexical decision and synonyms tasks loaded strongly on the first factor, which appeared to index the breadth of participants' semantic knowledge. The two semantic control tasks and the verbal fluency tasks loaded on a second factor. All of these tests require controlled retrieval and use of semantic knowledge. The third factor had strong loadings for the Wisconsin card-sorting task and the incongruent feature task. This factor may therefore capture aspects of domain-general executive function that are not specific to semantics.

The correlation matrix for test scores in the young group is shown in Table 6 (note that correlations with age and educational level were not computed because there was little variation in these characteristics in the young group). As in the older group, there was a strong positive relationship between the two representation tests. There were also positive associations between these tests and the weak association task, although no correlation with the incongruent feature task. There was, however, a significant positive association between the incongruent feature task and the Wisconsin card-sorting task.

The results of the principal components analysis for the young group are shown in Table 8. There were three factors with eigenvalues greater than one, which together accounted for 70% of the variance in test scores. The lexical decision and synonym tasks loaded strongly on the first factor but, unlike the older group, the weak association task also loaded strongly on this factor. The second factor had strong loadings for the two verbal fluency tasks. However, the two semantic control tasks did not load on this factor. Finally, the

third factor had strong loadings for the incongruent features and Wisconsin card-sorting tests, again suggesting that both may rely on domain-general executive resources.

Table 7: Principal components analysis for the older group

	Factor 1	Factor 2	Factor 3
Lexical Decision	**.94**	.09	.17
Synonyms	**.94**	.14	-.07
Weak Associations	.34	**.62**	-.06
Incongruent Features	.24	**.40**	**.60**
Category fluency	.08	**.76**	.24
Letter fluency	-.03	**.82**	-.32
Wisconsin card-sorting	-.07	-.24	**.84**

Factor loadings > 0.4 are shown in bold.

Table 8: Principal components analysis for the young group

	Factor 1	Factor 2	Factor 3
Lexical Decision	**.92**	.06	.06
Synonyms	**.76**	.04	.14
Weak Associations	**.76**	.12	.00
Incongruent Features	.13	-.05	**.83**
Category fluency	.03	**.85**	.06
Letter fluency	.15	**.79**	.03
Wisconsin card-sorting	.02	.15	**.85**

Factor loadings > 0.4 are shown in bold.

Discussion

This study investigated relationships between semantic knowledge, semantic control and non-semantic executive control in young and older adults. Little is known about the relationships between these capabilities in healthy adults. However, there are clear neural dissociations between the representation of semantic knowledge and processes that control access to and use of this knowledge. Supporting proposals from cognitive neuroscience (Badre et al., 2005; Nagel et al., 2008), the present study found evidence for two distinct forms of semantic control – controlled retrieval of knowledge and selection among competing representations. Performance on tests tapping these two abilities was independent of one another. In fact, while controlled retrieval ability was superior in older people, there was a

clear decrement in semantic selection ability, with older adults less able to ignore irrelevant semantic associations in favour of task-relevant aspects of knowledge. This was observed in comparisons of young and older adults and in correlational analyses of age effects within the older group (between 61 and 91 years). In both groups, semantic selection ability was linked with performance on a non-semantic executive function task, the Wisconsin card-sorting test, which also requires inhibition of irrelevant aspects of stimuli. In contrast to this specific decline in executively-demanding semantic tasks, older people had markedly larger stores of semantic knowledge, out-performing their younger counterparts on tests of knowledge for low frequency words. Taken together, these findings suggest three distinct contributors to semantic cognition: a store of representations which accumulates throughout the lifespan, processes for controlled retrieval of weakly related concepts from this store which are also more developed in later life, and domain-general executive selection mechanisms that decline in old age.

Previous studies have observed that older people often perform better on semantic tests that probe vocabulary size (Nilsson, 2003; Park et al., 2002; Rönnlund et al., 2005; Salthouse, 2004; Verhaeghen, 2003). This effect was particularly striking in the present study: in addition to out-performing young people in accuracy, the older group matched them in reaction time, despite being slower to respond on a range of other tasks. These findings clearly indicate that older people have a more detailed store of knowledge representations that allow them to more successfully recognise and determine the meanings of low frequency words. In line with previous studies (Verhaeghen, 2003), older adults who had spent greater time in education exhibited broader semantic knowledge, indicating that educational experience plays an important part in determining the eventual size of the knowledge store. Consistent with this conclusion, a recent study found that the volume of the ventral temporal cortices in later life (a key neural substrate for the representation of semantic knowledge; e.g., Patterson et al., 2007) was a predictor of performance on semantic knowledge tests, and that this effect was mediated by educational level (Hoffman et al., 2017). It is important to note, however, that the young and older groups did not differ in mean years of education, so general life experience must also contribute to the large disparity in knowledge between the two groups.

The weak association task was used to probe participants' ability to engage in controlled retrieval of less salient information from the semantic store. This aspect of control has been closely associated with anterior prefrontal cortex, which is thought to provide top-down constraint over the activation of knowledge represented in the temporal cortices

(Badre et al., 2005). This ability to regulate retrieval of semantic information was closely related to breadth of semantic knowledge in young participants. Those with more detailed representations were better at detecting weak associations between concepts, which underscores the close interaction between these aspects of semantic cognition. In older people this relationship was less strong, though still present. In this group, weak association performance patterned more closely with the semantic selection and verbal fluency tasks. However, weak association detection was not related to performance on the Wisconsin card-sorting test, suggesting it is distinct from other, domain-general executive functions. The association of improved controlled retrieval with broader semantic knowledge, observed both within and between age groups, suggests that individuals with greater reserves of semantic knowledge also develop more effective mechanisms for regulating the retrieval of information from this store.

In contrast to their enhanced ability to detect weak semantic associations, older adults showed a marked decline in semantic selection. This finding can be interpreted in the context of old-age deficits in inhibitory function and interference resolution across a range of tasks (Borella, Carretti, & De Beni, 2008; Hasher & Zacks, 1988; Salthouse & Meinz, 1995). Domain-general executive mechanisms are therefore likely to be involved in this aspect of semantic processing, as implied by previous neuroimaging investigations (Badre & Wagner, 2007). Supporting this conclusion, there were strong correlations between semantic selection ability and Wisconsin card-sorting performance in young people. The two tests also patterned together in principal components analysis in the older group, suggesting a common basis. An inhibitory account of these findings would hold that older people have difficulty suppressing strong pre-existing semantic associations in the incongruent condition of the feature association task, as well as inhibiting attention to irrelevant aspects of the stimuli in the Wisconsin card-sorting task (Buchsbaum, Greer, Chang, & Berman, 2005). Importantly, this account would not predict old-age decrements in the weak associations task, as there were no irrelevant associations to ignore in this task. It should be noted that results from the Erikson flanker task provided no evidence for impaired inhibitory function in older people, but this task has been criticised as a poor indicator of individual differences in inhibition (Salthouse, 2010).

In addition to domain-general inhibitory deficits, it is important to consider factors within the semantic system that might contribute to age-related decline in semantic selection. It is possible that the more extensive semantic knowledge of older participants exacerbates

their problems with semantic selection, since they have a richer network of semantic associations that could potentially cause interference. This hypothesis makes two predictions. First, older people should perform more poorly than young people on tasks requiring selection among competing semantic representations, as was observed. Second, within each age group, those with broader semantic knowledge should display poorer semantic selection ability. There was no evidence for this second effect in the present study, which suggests that greater knowledge does not necessarily result in increased interference between concepts. An alternative possibility is that individuals with richer semantic knowledge develop more effective selection mechanisms to manage potential interference between concepts, as has been observed in bilinguals (Bialystok, Craik, & Luk, 2008).

Finally, the semantic selection deficits observed in the older group cannot be attributed to reductions in general processing speed in later life, as participants were given unlimited time to complete the semantic tasks. Indeed, RT analyses indicated that the older participants took much longer to complete the incongruent condition requiring semantic selection and, despite this extra time taken, were less accurate than young participants. This is an important point because a number of previous studies have contrasted sharp declines in speed of processing with relative preservation of knowledge in older age, and have assessed the influence of these factors on complex verbal abilities, such as performance on verbal fluency tasks (Bryan, Luszcz, & Crawford, 1997; Ghisletta & Lindenberger, 2003; Salthouse, 1993). Rather than pitting knowledge against speed, the present study contrasted semantic knowledge with semantic control. However, we also found divergent age-related changes, which related to performance on other verbal tasks. Verbal fluency scores in the older participants were closely related to performance on the weak associations task, which indexes controlled retrieval of knowledge. In addition, in principal components analysis their scores on the fluency tasks loaded on the same factor as both semantic control tasks. Perhaps this is unsurprising, since verbal fluency tasks are widely assumed to tax the executive control system in addition to verbal knowledge reserves (Hoffman et al., 2017; Lezak, 2004; Salthouse, Atkinson, & Berish, 2003; Shao, Janse, Visser, & Meyer, 2014). Specifically, a strong ability to retrieve weak semantic associates is likely to boost the number of potential responses available in verbal fluency, while selection and inhibition processes are important for avoiding item repetition or out-of-category responses (Rogers, Patterson, Jefferies, & Lambon Ralph, 2015). There was no clear evidence for age-related declines in verbal fluency in the present study: category fluency scores were significantly lower in the older group but letter fluency

scores were higher. One possible explanation for this net stability is that the negative impact of impaired semantic selection in old age is offset by increased reserves of knowledge and improved controlled retrieval. More generally, the major contribution of this study is to indicate that semantic cognition relies on multiple distinct capabilities that vary substantially across individuals and age groups. This opens the possibility for future studies to explore the interplay between these elements of semantic cognition and their functional consequences for complex verbal and non-verbal semantic behaviours.

References

Allen, C. M., Martin, R. C., & Martin, N. (2012). Relations between short-term memory deficits, semantic processing, and executive function. *Aphasiology, 26*(3-4), 428-461. doi:Doi 10.1080/02687038.2011.617436

Anderson, J. R. (1974). Retrieval of propositional information from long-term memory. *Cognitive Psychology, 6*(4), 451-474.

Anderson, J. R., & Reder, L. M. (1999). The fan effect: New results and new theories. *Journal of Experimental Psychology-General, 128*(2), 186-197.

Baddeley, A., Emslie, H., & Smith, I. N. (1992). *The Speed and Capacity of Language Processing test*. Bury St Edmunds: Thames Valley Test Company.

Badre, D., Poldrack, R. A., Pare-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron, 47*(6), 907-918.

Badre, D., & Wagner, A. D. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. *Behavioral and Cognitive Neuroscience Reviews, 1*, 206-218.

Badre, D., & Wagner, A. D. (2005). Frontal lobe mechanisms that resolve proactive interference. *Cerebral Cortex, 15*(12), 2003-2012.

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia, 45*(13), 2883-2901.

Bialystok, E., Craik, F., & Luk, G. (2008). Cognitive control and lexical access in younger and older bilinguals. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34*(4), 859.

Borella, E., Carretti, B., & De Beni, R. (2008). Working memory and inhibition across the adult life-span. *Acta Psychologica, 128*(1), 33-44.

Bryan, J., Luszcz, M. A., & Crawford, J. (1997). Verbal knowledge and speed of information processing as mediators of age differences in verbal fluency performance among older adults. *Psychol Aging, 12*(3), 473.

Brysbaert, M., Warriner, A. B., & Kuperman, V. (2014). Concreteness ratings for 40 thousand generally known English word lemmas. *Behavior Research Methods, 46*(3), 904-911.

Buchsbaum, B. R., Greer, S., Chang, W. L., & Berman, K. F. (2005). Meta-analysis of neuroimaging studies of the Wisconsin Card-Sorting task and component processes. *Human Brain Mapping, 25*(1), 35-45.

Cohen, J. D., Dunbar, K., & McClelland, J. L. (1990). On the control of automatic processes: a parallel distributed processing account of the Stroop effect. *Psychological Review, 97*(3), 332.

Deary, I. J., Penke, L., & Johnson, W. (2010). The neuroscience of human intelligence differences. *Nature Reviews Neuroscience, 11*(3), 201-211.

Dobbins, I. G., & Wagner, A. D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex, 15*(11), 1768-1778.

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences, 14*(4), 172-179.

Eriksen, C. W. (1995). The flankers task and response competition: A useful tool for investigating a variety of cognitive problems. *Visual Selective Attention*, 101-118.

Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences, 110*(41), 16616-16621.

Ghisletta, P., & Lindenberger, U. (2003). Age-based structural dynamics between perceptual speed and knowledge in the Berlin Aging Study: direct evidence for ability dedifferentiation in old age. *Psychol Aging, 18*(4), 696.

Gold, B. T., Balota, D. A., Jones, S. J., Powell, D. K., Smith, C. D., & Andersen, A. H. (2006). Dissociation of automatic and strategic lexical-semantics: functional magnetic resonance imaging evidence for differing roles of multiple frontotemporal regions. *Journal of Neuroscience, 26*(24), 6523-6532. doi:10.1523/JNEUROSCI.0808-06.2006

Gottfredson, L. S. (1997). Mainstream science on intelligence: An editorial with 52 signatories, history, and bibliography: JAI.

Grady, C. (2012). The cognitive neuroscience of ageing. *Nature Reviews Neuroscience, 13*(7), 491-505.

Guo, C. C., Gorno-Tempini, M. L., Gesierich, B., Henry, M., Trujillo, A., Shany-Ur, T., . . . Seeley, W. W. (2013). Anterior temporal lobe degeneration produces widespread network-driven dysfunction. *Brain, 136*(Pt 10), 2979-2991. doi:10.1093/brain/awt222

Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. *Psychology of learning and motivation, 22*, 193-225.

Hazeltine, E., Bunge, S. A., Scanlon, M. D., & Gabrieli, J. D. (2003). Material-dependent and material-independent selection processes in the frontal and parietal lobes: an event-

related fMRI investigation of response competition. *Neuropsychologia, 41*(9), 1208-1217.

Hoffman, P. (2016). The meaning of "life" and other abstract words: Insights from neuropsychology. *J Neuropsychol, 10*, 317-343.

Hoffman, P., Binney, R. J., & Lambon Ralph, M. A. (2015). Differing contributions of inferior prefrontal and anterior temporal cortex to concrete and abstract conceptual knowledge. *Cortex, 63*, 250-265. doi:10.1016/j.cortex.2014.09.001

Hoffman, P., Cox, S. R., Dykiert, D., Maniega, S. M., Hernández, M. C. V., Bastin, M. E., . . . Deary, I. J. (2017). Brain grey and white matter predictors of verbal ability traits in older age: The Lothian Birth Cohort 1936. *Neuroimage*.

Hoffman, P., Lambon Ralph, M. A., & Rogers, T. T. (2013). Semantic diversity: A measure of semantic ambiguity based on variability in the contextual usage of words. *Behavior Research Methods, 45*(3), 718-730.

Hoffman, P., Rogers, T. T., & Lambon Ralph, M. A. (2011). Semantic diversity accounts for the "missing" word frequency effect in stroke aphasia: Insights using a novel method to quantify contextual variability in meaning. *Journal of Cognitive Neuroscience, 23*(9), 2432-2446.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics*, 65-70.

Humphreys, G. F., Hoffman, P., Visser, M., Binney, R. J., & Lambon Ralph, M. A. (2015). Establishing task- and modality-dependent dissociations between the semantic and default mode networks. *Proceedings of the National Academy of Sciences of the United States of America, 112*(25), 7857-7862.

Jackson, R. L., Hoffman, P., Pobric, G., & Lambon Ralph, M. A. (2016). The Semantic Network at Work and Rest: Differential Connectivity of Anterior Temporal Lobe Subregions. *The Journal of Neuroscience, 36*(5), 1490-1501.

January, D., Trueswell, J. C., & Thompson-Schill, S. L. (2009). Co-localization of Stroop and syntactic ambiguity resolution in Broca's area: Implications for the neural basis of sentence processing. *Journal of Cognitive Neuroscience, 21*(12), 2434-2444.

Jefferies, E. (2013). The neural basis of semantic cognition: Converging evidence from neuropsychology, neuroimaging and TMS. *Cortex, 49*, 611-625.

Jefferies, E., & Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: a case-series comparison. *Brain, 129*(Pt 8), 2132-2147. doi:10.1093/brain/awl153

Jung, J., Cloutman, L. L., Binney, R. J., & Ralph, M. A. L. (2016). The structural connectivity of higher order association cortices reflects human functional brain networks. *Cortex*.

Kan, I. P., & Thompson-Schill, S. L. (2004). Selection from perceptual and conceptual representations. *Cognitive, Affective, & Behavioral Neuroscience, 4*(4), 466-482.

Krieger-Redwood, K., Teige, C., Davey, J., Hymers, M., & Jefferies, E. (2015). Conceptual control across modalities: graded specialisation for pictures and words in inferior frontal and posterior temporal cortex. *Neuropsychologia, 76*, 92-107.

Kuperman, V., Stadthagen-Gonzalez, H., & Brysbaert, M. (2012). Age-of-acquisition ratings for 30,000 English words. *Behavior Research Methods, 44*(4), 978-990.

Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience, 18*, 42-55. doi:10.1038/nrn.2016.150

Lambon Ralph, M. A., & Patterson, K. (2008). Generalisation and differentiation in semantic memory. *Annals of the New York Academy of Sciences, 1124*, 61-76.

Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: The latent semantic analysis theory of acquisition, induction and representation of knowledge. *Psychological Review, 104*, 211-240.

Lezak, M. D. (2004). *Neuropsychological assessment*: Oxford University Press, USA.

Mion, M., Patterson, K., Acosta-Cabronero, J., Pengas, G., Izquierdo-Garcia, D., Hong, Y. T., . . . Nestor, P. J. (2010). What the left and right anterior fusiform gyri tell us about semantic memory. *Brain, 133*(11), 3256-3268. doi:10.1093/brain/awq272

Mueller, S. T., & Piper, B. J. (2014). The psychology experiment building language (PEBL) and PEBL test battery. *Journal of neuroscience methods, 222*, 250-259.

Nagel, I. E., Schumacher, E. H., Goebel, R., & D'Esposito, M. (2008). Functional MRI investigation of verbal selection mechanisms in lateral prefrontal cortex. *Neuroimage, 43*(4), 801-807.

Nilsson, L. G. (2003). Memory function in normal aging. *Acta Neurologica Scandinavica, 107*(s179), 7-13.

Noonan, K. A., Jefferies, E., Corbett, F., & Lambon Ralph, M. A. (2010). Elucidating the nature of deregulated semantic cognition in semantic aphasia: Evidence for the roles

of the prefrontal and temporoparietal cortices. *Journal of Cognitive Neuroscience, 22*, 1597-1613.

Noonan, K. A., Jefferies, E., Visser, M., & Lambon Ralph, M. A. (2013). Going beyond Inferior Prefrontal Involvement in Semantic Control: Evidence for the Additional Contribution of Dorsal Angular Gyrus and Posterior Middle Temporal Cortex. *Journal of Cognitive Neuroscience, 25*(11), 1824-1850.

Nyberg, L., Bäckman, L., Erngrund, K., Olofsson, U., & Nilsson, L.-G. (1996). Age differences in episodic memory, semantic memory, and priming: Relationships to demographic, intellectual, and biological factors. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 51*(4), P234-P240.

Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychol Aging, 17*(2), 299-320. doi:10.1037//0882-7974.17.2.299

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8*(12), 976-987.

Pobric, G., Jefferies, E., & Lambon Ralph, M. A. (2007). Anterior temporal lobes mediate semantic representation: mimicking semantic dementia by using rTMS in normal participants. *Proc Natl Acad Sci U S A, 104*(50), 20137-20141. doi:10.1073/pnas.0707383104

Raven, J. C., Raven, J. E., & Court, J. H. (1989). *Mill Hill vocabulary scale*: Psychological Corporation.

Reitan, R. M. (1992). *Trail Making Test: Manual for administration and scoring*: Reitan Neuropsychology Laboratory.

Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex, 15*(8), 1261-1269.

Rogers, T. T., Patterson, K., Jefferies, E., & Lambon Ralph, M. A. (2015). Disorders of representation and control in semantic cognition: Effects of familiarity, typicality, and specificity. *Neuropsychologia, 76*, 220-239.

Rönnlund, M., Nyberg, L., Bäckman, L., & Nilsson, L.-G. (2005). Stability, growth, and decline in adult life span development of declarative memory: cross-sectional and longitudinal data from a population-based study. *Psychol Aging, 20*(1), 3.

Saffran, E. M. (2000). The organization of semantic memory: In support of a distributed model. *Brain and Language, 71*(1), 204-212.

Salthouse, T. A. (1993). Speed and knowledge as determinants of adult age differences in verbal tasks. *Journal of gerontology, 48*(1), P29-P36.

Salthouse, T. A. (2004). Localizing age-related individual differences in a hierarchical structure. *Intelligence, 32*(6), 541-561.

Salthouse, T. A. (2010). Is flanker-based inhibition related to age? Identifying specific influences of individual differences on neurocognitive variables. *Brain and Cognition, 73*(1), 51-61.

Salthouse, T. A., Atkinson, T. M., & Berish, D. E. (2003). Executive functioning as a potential mediator of age-related cognitive decline in normal adults. *Journal of Experimental Psychology-General, 132*(4), 566-594. doi:Doi 10.1037/0096-3445.132.4.566

Salthouse, T. A., & Meinz, E. J. (1995). Aging, inhibition, working memory, and speed. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 50*(6), P297-P306.

Salthouse, T. A., & Miles, J. D. (2002). Aging and time-sharing aspects of executive control. *Memory & Cognition, 30*(4), 572-582.

Shao, Z., Janse, E., Visser, K., & Meyer, A. S. (2014). What do verbal fluency tasks measure? Predictors of verbal fluency performance in older adults. *Frontiers in Psychology, 5*.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences of the United States of America, 94*, 14792-14797.

Treitz, F. H., Heyder, K., & Daum, I. (2007). Differential course of executive control changes during normal aging. *Aging, Neuropsychology, and Cognition, 14*(4), 370-393.

Van Heuven, W. J., Mandera, P., Keuleers, E., & Brysbaert, M. (2014). SUBTLEX-UK: A new and improved word frequency database for British English. *The Quarterly Journal of Experimental Psychology, 67*(6), 1176-1190.

Verhaeghen, P. (2003). Aging and vocabulary score: A meta-analysis. *Psychol Aging, 18*(2), 332-339. doi:10.1037/0882-7974.18.2.332

Verhaeghen, P., & Cerella, J. (2002). Aging, executive control, and attention: a review of meta-analyses. *Neuroscience & Biobehavioral Reviews, 26*(7), 849-857.

Von Der Heide, R. J., Skipper, L. M., Klobusicky, E., & Olson, I. R. (2013). Dissecting the uncinate fasciculus: disorders, controversies and a hypothesis. *Brain, 136*(Pt 6), 1692-1707. doi:10.1093/brain/awt094

Warrington, E. K., & Cipolotti, L. (1996). Word comprehension: The distinction between refractory and storage impairments. *Brain, 119*, 611-625.

Whitney, C., Jefferies, E., & Kircher, T. (2011). Heterogeneity of the left temporal lobe in semantic representation and control: priming multiple versus single meanings of ambiguous words. *Cereb Cortex, 21*(4), 831-844. doi:10.1093/cercor/bhq148

Yee, E., & Thompson-Schill, S. L. (2016). Putting concepts into context. *Psychonomic Bulletin & Review, 23*(4), 1015-1027.