Divergent effects of healthy ageing on semantic knowledge and control: Evidence from novel comparisons with semantically-impaired patients

Paul HOFFMAN

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

* 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

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Abstract

Effective use of semantic knowledge requires a set of conceptual representations as well as control processes which ensure that currently-relevant aspects of this knowledge are retrieved and selected. It is well-established that levels of semantic knowledge increase across the lifespan. However, the effects of ageing on semantic control processes have not been assessed. I addressed this issue by comparing the performance profiles of young and older people on a verbal comprehension test. Two sets of variables were used to predict accuracy and RT in each age group: (a) the psycholinguistic properties of words being probed, (b) the scores of two sets of semantically-impaired neuropsychological patients who had completed the test previously. Young people demonstrated poor performance for low frequency and abstract words, suggesting that they had difficulty processing words with intrinsically weak semantic representations. Indeed, performance in this group was strongly predicted by the scores of patients with semantic dementia, who suffer from degradation of semantic knowledge. In contrast, older adults performed poorly on trials where the target semantic relationship was weak and distractor relationships strong – conditions which require high levels of controlled processing. Their performance was better predicted by the scores of patients with semantic control deficits. These findings indicate that the effects of ageing on semantic cognition are more complex than has previously been assumed. While older people have larger stores of knowledge than young people, they are less skilled at exercising control over the activation of this knowledge.

Keywords: semantic cognition; cognitive ageing; semantic dementia; semantic aphasia.

Introduction

Semantic knowledge, for the meanings of words and properties of objects, shapes our understanding of the environment and guides our behaviour. In addition to storing this information in memory, effective semantic cognition – that is, the ability to use semantic knowledge to complete cognitive tasks – requires us to *control* how we retrieve and use it in specific situations (Badre & Wagner, 2002; Hoffman, 2016; Jefferies, 2013; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Yee & Thompson-Schill, 2016). Cognitive control over the activation and selection of semantic information is 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. This ability to retrieve task-relevant semantic information while avoiding interference from competing elements of knowledge is often termed "semantic control".

How do semantic abilities change across the lifespan? There is good evidence that the amount of semantic knowledge people have, as indexed by their scores on vocabulary tests, increases as they grow older and remains relatively stable into old age (Grady, 2012; Nilsson, 2003; Nyberg, Bäckman, Erngrund, Olofsson, & Nilsson, 1996; Park et al., 2002; Rönnlund, Nyberg, Bäckman, & Nilsson, 2005; Salthouse, 2004). A meta-analysis of 210 studies indicated that adults aged over 60 score substantially higher on vocabulary tests than young adults (Verhaeghen, 2003). This effect is typically explained in terms of older participants continuing to add to their semantic knowledge store throughout their lives. Consistent with this conclusion, greater time spent in formal education appears to account for much of the age effect (Verhaeghen, 2003). However, while it seems clear that older people have a larger repository of semantic knowledge than young people, the effect of ageing on semantic control processes has rarely been investigated. Other forms of cognitive control, outside the semantic domain, tend to deteriorate as people grow older (Hasher & Zacks, 1988; Salthouse & Miles, 2002; Treitz, Heyder, & Daum, 2007; Verhaeghen & Cerella, 2002) and it is possible that semantic control suffers a similar fate. This remains a largely unexplored possibility in the cognitive ageing literature.

Semantic control processes have been more of a focus in the neuropsychological literature, where a number of studies have indicated that semantic knowledge representations and the semantic control system can be impaired independently following brain damage (Jefferies & Lambon Ralph, 2006; Rogers, Patterson, Jefferies, & Lambon Ralph, 2015; Warrington & Cipolotti, 1996). The clearest example of impairment to semantic knowledge is the syndrome of semantic dementia (SD), in which patients exhibit a progressive and highly selective loss of semantic representations (Patterson, Nestor, & Rogers, 2007). The erosion of semantic knowledge in this condition follows a predictable pattern whereby patients are more likely to retain information that is experienced more frequently, is more typical of its domain and is shared across many different concepts (Funnell, 1995; Hoffman, Jones, & Lambon Ralph, 2012; Mayberry, Sage, & Lambon Ralph, 2011; Rogers et al., 2015; Woollams, Cooper-Pye, Hodges, & Patterson, 2008). Such information is considered to be more represented more strongly in the semantic store (Rogers et al., 2004; Rogers & McClelland, 2004). Some studies have also found that SD patients have poorer knowledge for abstract words, relative to concrete ones (Hoffman & Lambon Ralph, 2011; Jefferies, Patterson, Jones, & Lambon Ralph, 2009), which has been attributed to concrete words benefiting from a richer set of sensory-motor associations (Hoffman, 2016). The loss of semantic knowledge in this condition appears to be a direct consequence of atrophy to the anterior temporal cortices (Butler, Brambati, Miller, & Gorno-Tempini, 2009; Mion et al., 2010). Studies using functional neuroimaging and brain stimulation in healthy individuals also implicate this region in the representation of semantic knowledge (Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015; Pobric, Jefferies, & Lambon Ralph, 2007; Rogers et al., 2006; Visser, Jefferies, & Lambon Ralph, 2010).

The deterioration of semantic knowledge in SD has been contrasted with multimodal semantic deficits that can occur following left-hemisphere stroke (Crutch & Warrington, 2008; Jefferies & Lambon Ralph, 2006; Rogers et al., 2015; Warrington & Cipolotti, 1996). Stroke is less likely to affect the anterior temporal cortices, which benefit from a double arterial blood supply (Gloor, 1997). Instead, semantic deficits in this group of patients, who are often termed semantic aphasics (SA), result from prefrontal and posterior temporoparietal damage (Noonan, Jefferies, Corbett, & Lambon Ralph, 2010). Consistent with this different locus of damage, semantic knowledge representations appear to be intact in SA patients. Instead, their semantic deficits stem from difficulty in controlling how this knowledge is accessed and selected according to current task demands. For example, they have difficulty identifying meaningful relationships between words where they do not share a strong automatic association (e.g., they can detect the semantic relationship between *necklace* and *earring* but not between *necklace* and *trousers*) (Noonan et al., 2010). They also perform poorly when required to ignore strong, pre-potent semantic associations that are irrelevant to the task at hand. For example, in a synonym matching task they will erroneously select antonyms if they have a stronger relationship with the probe (e.g., matching *major* with *minor* rather than *important*). Thus, SA patients find semantic tasks particularly challenging when the target semantic relationship is weak and any irrelevant non-target relationships are strong (Jefferies & Lambon Ralph, 2006). Functional neuroimaging studies indicate that these conditions also elicit the strongest activation in prefrontal and temporoparietal regions associated with control of semantic processing (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Noonan, Jefferies, Visser, & Lambon Ralph, 2013; Thompson-Schill et al., 1997).

Like SD patients, individuals with SA find it easier to understand highly concrete words (Hoffman, Jefferies, & Lambon Ralph, 2010) but, unlike SD patients, they show little or no effects of frequency in their comprehension (Almaghyuli, Thompson, Lambon Ralph, & Jefferies, 2012; Hoffman, Jefferies, & Lambon Ralph, 2011a; Hoffman, Rogers, & Lambon Ralph, 2011b; Warrington & Cipolotti, 1996). Instead, they show particularly poor comprehension of words that are semantically diverse, meaning that they can be used a wide variety of different contexts (Hoffman et al., 2011b). The contextual promiscuity of these words appears to pose problems for SA patients because they have difficulty selecting which aspect of the word's meaning is relevant for the current context (see also Noonan et al., 2010). In contrast, semantic diversity has no effect on comprehension in SD patients (Hoffman et al., 2011b).

Comparative studies of SD and SA patients have provided us with a clear model of the characteristics of semantic processing that are associated with weakness in either the representation of semantic knowledge or in its controlled processing. The present study used these insights to investigate areas of semantic weakness in healthy young and older adults. Participants completed a forced-choice verbal comprehension task in which they were asked to identify the synonyms of 96 words. The aim of the study was to investigate which factors influenced performance in each group. As summarised above, neuropsychological deficits in semantic knowledge and control are associated with sensitivity to different psycholinguistic variables. Accordingly, the first set of we investigated which psycholinguistic properties best predicted performance in young and older people. We predicted that young people, like SD patients, would show larger effects of word frequency, as they are generally assumed to have a less developed store of semantic representations. Conversely, if older people have difficulties in the control of semantic processing, we would expect the factors influencing their performance to be similar to those that predict comprehension in SA: i.e., the semantic diversity of the words probed and the relative strength of target and non-target semantic relationships. As a second test of these hypotheses, I used previously-published data from 26 SD and SA patients, who completed the same comprehension task, to predict performance in healthy participants. The expectation was that young people would perform poorly on trials that SD patients found particularly difficult, due to their under-developed semantic representations. Conversely, if older people have difficulties with semantic control, we would expect them to perform worst on the trials that SA patients frequently failed.

Method

Participants: Twenty-seven young adults, aged between 18 and 22, were recruited from the undergraduate Psychology course at the University of Edinburgh and participated in the study in exchange for course credit. Twenty-seven older adults, aged between 61 and 90, were recruited from the Psychology department's volunteer panel. 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 1. Young and older adults did not differ significantly in years of education completed ($t(52) = 1.12$, $p = 0.27$).

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. Task-switching ability was assessed using the Trail-making task (Reitan, 1992). Executive function was also assessed with a computerised version of the Wisconsin Card-Sorting Test, consisting of 64 trials (Mueller & Piper, 2014). 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). Participants completed two standardised tests of vocabulary knowledge: the Spot-the-Word Test from the Speed and Capacity of Language Processing battery (Baddeley, Emslie, & Smith, 1992) and a modified version of the Mill Hill vocabulary test (Raven, Raven, & Court, 1989), in which participants were asked to select the synonyms of low-frequency words from four alternatives.

Materials: Participants completed a 96-item synonym judgement test, which has been used in a number of previous studies to assess verbal comprehension in healthy and impaired populations (e.g., Almaghyuli et al., 2012; Hoffman & Lambon Ralph, 2011; Hoffman et al., 2011b; Jefferies et al., 2009). On each trial, participants are presented with a probe word and asked to select which of three alternatives is most closely related in meaning to the probe (see Figure 1 for examples). The test was designed to vary the frequency and imageability of the words probed in a 2 x 3 factorial design. In the present study, these variables were entered into model as parametric predictors of performance, along with others (see below).

Procedure: The synonym judgement task was presented on a PC running E-prime software. Each trial began with a fixation cross presented for 500ms. The probe then appeared in the centre of the screen with the three options in a line below. Participants indicated their choice by button press and were instructed to respond as quickly as possible without making mistakes. No time limit was placed on responses. When a response was registered, the next trial began after a 500ms delay. The position of the target (left, centre, right) was randomised on each trial. The order of trials was also randomised for each participant. The main test was preceded by ten practice trials.

Analyses: Analyses were performed on accuracy and RT data. T-tests were first performed to test for group differences on the task as a whole. Subsequent analyses used mixed effects models to predict accuracy and RT at the level of individual trials. The first set of analyses used the psycholinguistic properties of the trials as predictors. Separate mixed models were estimated for accuracy and RT in young and older participants. In addition, combined models including all participants were estimated. These additionally included effects of age group and the interaction of group with the other predictors. The psycholinguistic predictors were as follows:

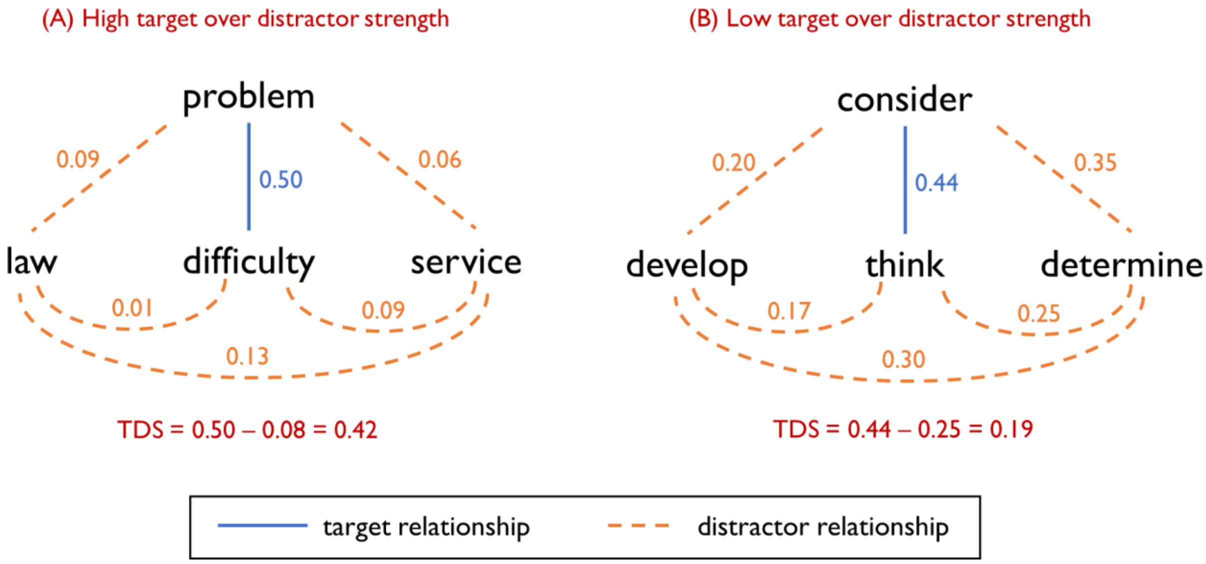
Frequency: Log word frequencies for the probe items were obtained from the CELEX database (Baayen, Piepenbrock, & van Rijn, 1993).

Imageability: Imageability ratings for the probe items were taken from the MRC psycholinguistic database (Coltheart, 1981). These varied on a scale from 100 to 700.

Semantic diversity: Values for the probe items were obtained from Hoffman et al. (2013). This semantic diversity measure is based on a large corpus of natural language and indexes the degree to which a word is used in a wide range of different contexts in the corpus.

Target vs. distractor strength (TDS): This measure was devised for the present study and was designed to quantify characteristics of the test that influence the need for semantic control. The measure indexed the strength of the target semantic relationship on each trial, relative to irrelevant relationships involving the distractor items. Calculation of this measure for two example trials are shown in Figure 1. The strength of semantic relationships was estimated using distributed representations of word meanings obtained from the word2vec neural network, trained on the 100 billion word Google News dataset (Mikolov, Chen, Corrado, & Dean, 2013). In common with other distributional models of word meaning, including latent semantic analysis (Landauer & Dumais, 1997), the word2vec model represents words as high-dimensional vectors, where similarity in two words' vectors indicates that they appear in similar contexts, and thus are assumed to have related meanings. The word2vec vectors were used here as a recent study has shown that these outperform other available vector datasets in predicting human semantic judgements (Pereira, Gershman, Ritter, & Botvinick, 2016). The strength of the semantic relationship between two words was defined as the cosine similarity of their word2vec vectors. This value was calculated for all pairs of words in all trials. TDS was defined as the strength of the target relationship minus the mean of all distractor relationships. As outlined in the Introduction, semantic control demands are highest when the target semantic relationship is relatively weak and there is competition from strong distractor relationships. Thus, trials with low TDS values were assumed to place the greatest demands on control processes.

Figure 1: Examples of trials with high and low TDS values



The second set of analyses used scores from SD and SA patients as predictors of performance in healthy participants. This analysis used data from Hoffman et al. (2011b), who reported data on the 96-item synonym judgement from 13 SD and 13 SA patients. The proportion correct on each trial of the test was calculated for each patient group and these values were entered as predictors of healthy performance. Separate models were estimated for each age group as well as combined models that included effects of age group and its interactions with other predictors. Based on the established interpretation of semantic deficits in these two groups, we assumed that similarity between healthy performance and SD performance would indicate weakness in semantic knowledge, whereas greater similarity between healthy performance and the performance of SA patients would indicate weakness in semantic control processes. As an additional test of these effects, we identified a subset of 20 trials in which SD patients scored substantially more poorly than SA patients (SDworst) and a subset of 21 trials in which SA patients scored substantially more poorly than SD patients (SAworst). These subsets were defined by computing a difference score for each trial (SD proportion correct minus SA proportion correct) and selecting trials where the difference exceeded 0.15 in either direction.

Mixed effects models were constructed and tested using the recommendations of Barr et al. (2013). Linear models were specified for analyses of RT and logistic models for accuracy. We specified a maximal random effects structure for all models, including random intercepts for participants and items as well as random slopes for all predictors that varied within-participant or within-item. The following control predictors were included in RT models: trial order, position of target (left, centre, right), accuracy on previous trial (as errors typically lead to a pronounced slowing on the subsequent trial). Continuous predictors were standardised prior to entry in the model. The significance of effects was assessed by comparing the full model with a reduced model that was identical in every respect except for the exclusion of the effect of interest. Likelihood-ratio tests were used to determine whether the inclusion of the effect of interest significantly improved the fit of the model.

Table 1: Demographic information and mean test scores for young and older participants

	Young adults	Older adults
N	27	27
Age	18.9 (0.8)	75.4 (9.2)***
Sex M:F	10:17	8:19
Years of education	13.9 (0.8)	13.2 (3.0)
MMSE /30	28.6 (0.9)	28.5 (2.2)
Wisconsin card-sorting task /64	50.8 (6.0)***	35.3 (11.9)
Trails A time (s)	30.8 (10.7)*	37.4 (12.2)
Trails B time (s)	48.7 (13.1)***	70.4 (24.1)
Category fluency (items per category)	23.1 (5.5)	20.8 (5.0)
Letter fluency (items per category)	14.4 (5.0)	15.4 (5.3)
Spot the Word test /60	47.0 (3.8)	54.0 (3.4)***
Mill Hill test (modified) /44	16.6 (4.4)	27.2 (5.4)***

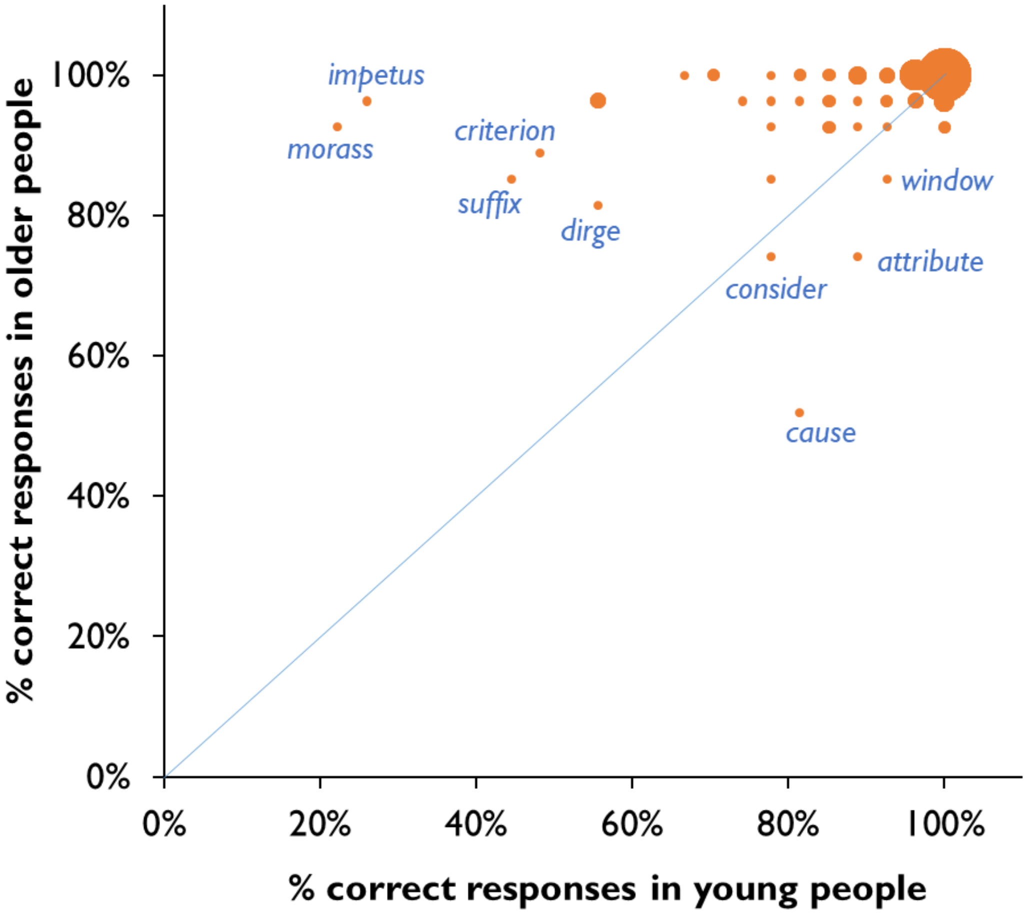
Standard deviations are shown in parentheses. Asterisks indicate the significance of t-tests comparing young and older adults. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Results

General cognitive assessments: Scores on the background tests are shown in Table 1. There were no group differences on the MMSE or the verbal fluency tasks. Young people outperformed older people on the Trail-making test, particularly part B which probes task-switching executive ability. The older group also demonstrated poorer executive function on the Wisconsin card-sorting test. In contrast, older people displayed significantly higher scores on the two tests of vocabulary, suggesting that they have greater reserves of semantic knowledge.

96-item synonym judgement test: Older people produced significantly more correct responses on the synonym judgement task (M = 96.2%; SD = 2.2) than young people (M = 89.9%; SD = 5.9; $t(52) = 4.73$, $p < 0.001$). However, the young group were significantly faster to respond (M = 2072ms; SD = 515) compared with the older group (M = 2718ms; SD = 926; $t(52) = 3.12$, $p = 0.003$). This is likely to reflect general age-related reductions in processing speed (Salthouse, 1996), rather than a semantic-specific effect. Our main interest in the present study was whether different factors influenced performance in the two age groups. Figure 2 provides the first indication that this may be the case. Accuracy on each of the 96 trials is plotted for the two groups. In both groups, the majority of trials were completed correctly by over 80% of participants. However, there were a small number of trials for which each group was less likely to give a correct response. Importantly, each group tended to fail on a different set of trials, as shown in Figure 2. Young people displayed notably poorer performance on trials that probed the meaning of low frequency words like *impetus* and *morass*, perhaps suggesting that they have yet to learn the meanings of these rarely-encountered words. In contrast, the older group performed most poorly on common words like *window* and *cause*. It is inconceivable that older people are unfamiliar with these words; instead it is likely that some aspect of the structure of these trials, such as competition between response options, which causes older people to find them particularly challenging. We test these hypotheses next.

Figure 2: Relationship between young and older accuracy for individual trials on the test



The size of the circles indicates the number of trials occupying each point. Trails falling below the diagonal were more likely to be completed correctly by young people, while trials above the diagonal were correct more often in older people.

Using psycholinguistic variables to predict performance in young and older individuals: Correlations between all performance measures and predictors (across items) are shown in Table 2. Accuracy in young and older people was positively correlated, but only moderately so (r = 0.34). This suggests that, as already noted, different factors may be influencing performance in each group. Indeed, the pattern of correlations between the performance measures and the other predictors appears markedly different for the two groups. There were, for example, strong correlations between word frequency and young people's accuracy and RT, but no such correlations for older people.

Table 2: Descriptive statistics and correlations for all dependent measures and predictors

	Mean (s.d.)	1	2	3	4	5	6	7	8	9
1. Young accuracy	0.89 (0.16)	--								
2. Older accuracy	0.97 (0.07)	.34***	--							
3. Young RT (ms)	2135 (680)	-.73***	-.39***	--						
4. Older RT (ms)	2785 (938)	-.46***	-.70***	.57***	--					
5. SD patients proportion correct	0.72 (0.23)	.59***	.35**	-.62***	-.36***	--				
6. SA patients proportion correct	0.72 (0.21)	.48***	.45***	-.53***	-.51***	.45***	--			
7. Probe frequency	1.32 (0.75)	.42***	-.02	-.43***	-.04	.54***	.04	--		
8. Imageability	450 (143)	.60***	.36***	-.67***	-.49***	.44***	.55***	.08	--	
9. Semantic diversity	1.65 (0.34)	-.00	-.24*	.05	.16	.06	-.38***	.60***	-.41***	--
10. TDS	0.34 (0.17)	.09	.29**	-.26*	-.41***	-.12	.15	-.19	.24*	-.23*

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Parameter estimates for the mixed effects models for accuracy are shown in Table 3. The modelled effects of each predictor are plotted in the top row of Figure 3. In the combined analysis of both groups, there were strong positive effects of frequency and imageability: overall, participants tended to produce more correct responses on trials involving high frequency and highly imageable words. Importantly, however, the effect of imageability interacted with group, with young people showing a larger influence of this variable. The group x frequency interaction did not reach statistical significance ($p = 0.12$), although only the young group showed a strong effect of this variable. In the combined analysis, the main effects of semantic diversity and TDS were somewhat weaker. However, the effect of TDS interacted with group. Older people were more strongly influenced by this variable, producing fewer correct responses on trials with low TDS values (i.e., when the target relationship was weak relative to distractor relationships). This variable did not influence the performance of young people. Older people also showed a tendency to respond less accurately to words with high semantic diversity, though this trend fell short of statistical significance ($p = 0.059$).

Parameter estimates for the RT models are presented in Table 4, with the modelled effects of the predictors shown in the bottom row of Figure 3. There was significant effects of frequency and imageability on RT. However, only young people were slower to respond to low frequency words, with older people showing no sign of such an effect. In contrast, both groups showed similar effects of imageability, responding more slowly to less concrete words. There was a strong effect of TDS in both groups, though this effect was significantly larger in the older people. Semantic diversity had no effect on RTs.

In summary, then, the performance of young people was most influenced by word frequency and imageability, two factors that have been linked with representational richness. In contrast, older people were more affected by the relative strength of target over distracting semantic relationships (i.e., TDS), in both accuracy and RT, and a trend towards less accurate responses to highly semantically diverse words. These results suggest weakness in controlled semantic processing in this group. These patterns were investigated further in the next section.

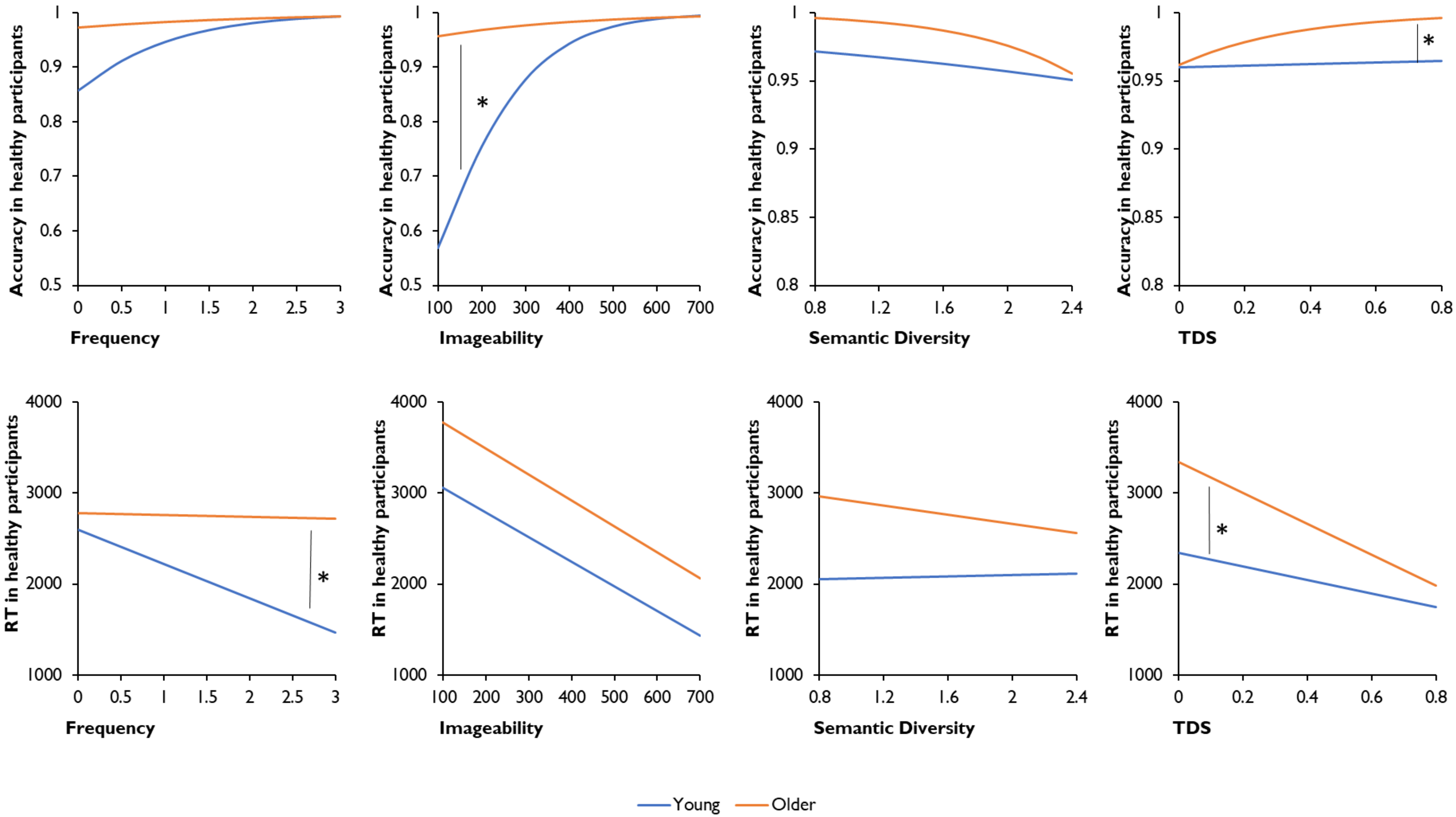
Table 3: Linear mixed effects models predicting healthy participant accuracy from psycholinguistic variables

	All			Young			Older		
	B	s.e.	*p*	B	s.e.	*p*	B	s.e.	*p*
Frequency	0.59	0.21	0.002	0.81	0.21	<0.001	0.36	0.29	0.19
Imageability	0.84	0.18	<0.001	1.21	0.18	<0.001	0.42	0.26	0.066
Semantic diversity	-0.33	0.22	0.097	-0.14	0.21	0.43	-0.54	0.32	0.059
TDS	0.27	0.15	0.055	0.04	0.14	0.78	0.42	0.22	0.033
Group	0.51	0.15	<0.001	----			----		
Group * Frequency	-0.22	0.15	0.12	----			----		
Group * Imageability	-0.37	0.13	0.003	----			----		
Group * Semantic diversity	-0.21	0.16	0.15	----			----		
Group * TDS	0.24	0.11	0.019	----			----		

Table 4: Linear mixed effects models predicting healthy participant RT from psycholinguistic variables

	All			Young			Older		
	B	s.e.	*p*	B	s.e.	*p*	B	s.e.	*p*
Frequency	-148	70.0	0.036	-278	60.1	<0.001	-14.8	105	0.89
Imageability	-393	66.6	<0.001	-373	60.1	<0.001	-407	100	<0.001
Semantic diversity	-36.2	75.8	0.63	11.0	64.9	0.87	-83.9	113	0.46
TDS	-210	53.1	<0.001	-126	44.0	0.005	-293	80.9	<0.001
Group	333	104	0.002	----			----		
Group * Frequency	133	47.5	0.006	----			----		
Group * Imageability	10.0	48.8	0.84	----			----		
Group * Semantic diversity	47.9	51.6	0.35	----			----		
Group * TDS	81.2	36.4	0.028	----			----		

Figure 3: Modelled effects of psycholinguistic variables on accuracy and RT. * *indicates a significant interaction between variable and group ($p < 0.05$).*



Using performance in SD and SA patients to predict performance in young and older individuals: Here, average accuracy of SD and SA patients on each trial of the test were used as predictors of performance in healthy individuals. Parameter estimates for the accuracy models are shown in Table 5 and the modelled effects of the predictors are presented in Figure 4. In the combined model, the scores of both SD and SA patients were strong predictors of accuracy in healthy individuals. However, the effect of the SD scores interacted with group. As shown in Figure 4, young people showed a strong effect of this predictor, performing more poorly on trials that few SD patients answered correctly. In contrast, this variable had no effect on the older group. Both groups showed similar effects of SA performance, producing fewer correct responses on trials that SA patients frequently failed.

The parameter estimates for models predicting RT data are shown in Table 6. Again, SD and SA scores were significant predictors, with healthy participants taking longer to respond on trials on which the patient groups performed poorly. Both predictors interacted with group with *p*-values that fell just short of 0.05. In both cases these effects were in the predicted direction. SD scores were a strong predictor of RTs in the young group, while they did not significantly predict RTs in older people. SA performance predicted RTs in both groups, but more strongly in the older group (see Figure 4).

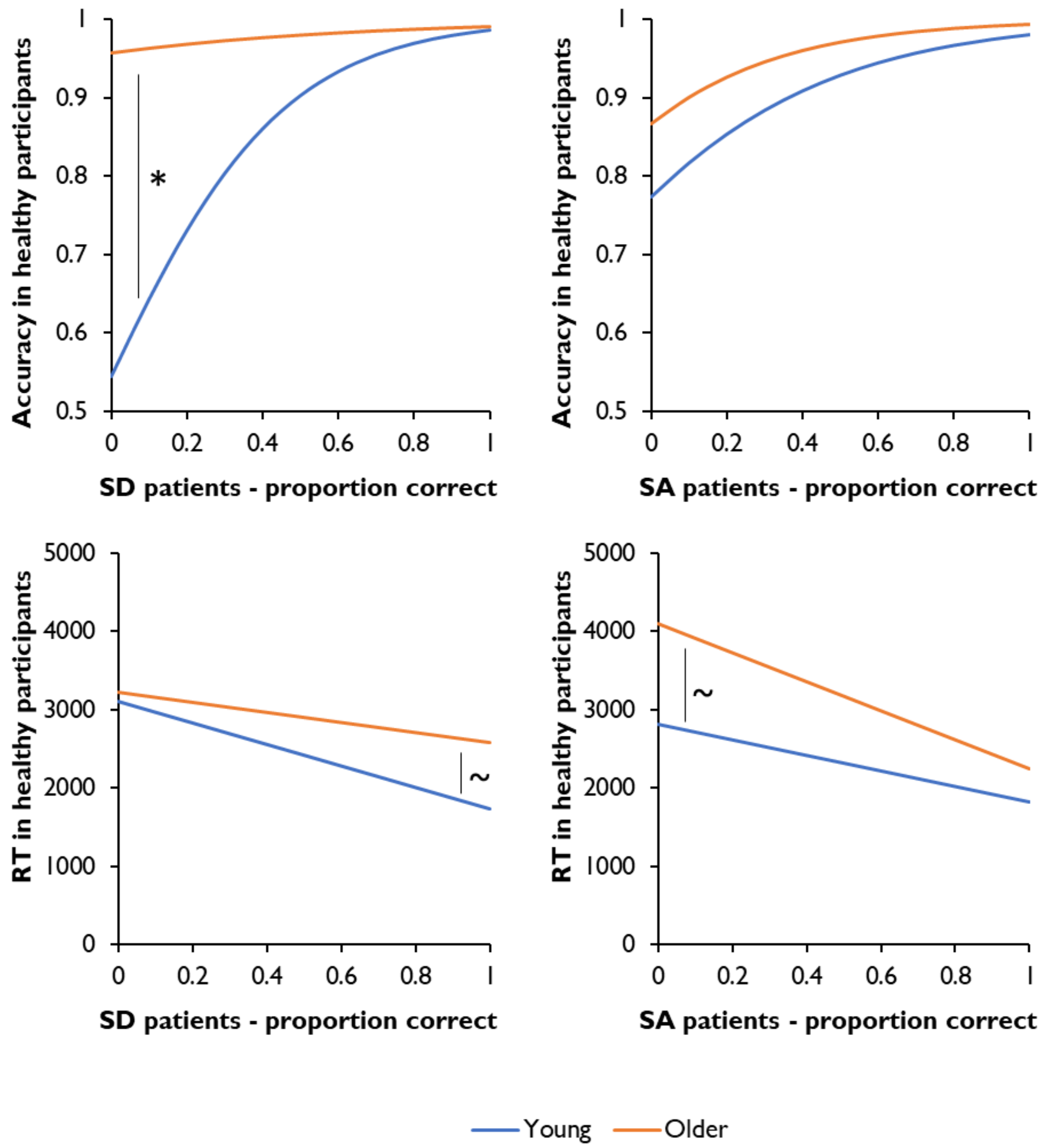
Table 5: Linear mixed effects models predicting healthy participant accuracy from patient scores

	All			Young			Older		
	B	s.e.	*p*	B	s.e.	*p*	B	s.e.	*p*
SD scores	0.65	0.16	<0.001	0.94	0.19	<0.001	0.35	0.20	0.082
SA scores	0.65	0.16	<0.001	0.58	0.19	0.002	0.66	0.21	0.002
Group	0.55	0.15	<0.001	----			----		
Group * SD scores	-0.29	0.12	0.017	----			----		
Group * SA scores	0.07	0.13	0.50	----			----		

Table 6: Linear mixed effects models predicting healthy participant RT from patient scores

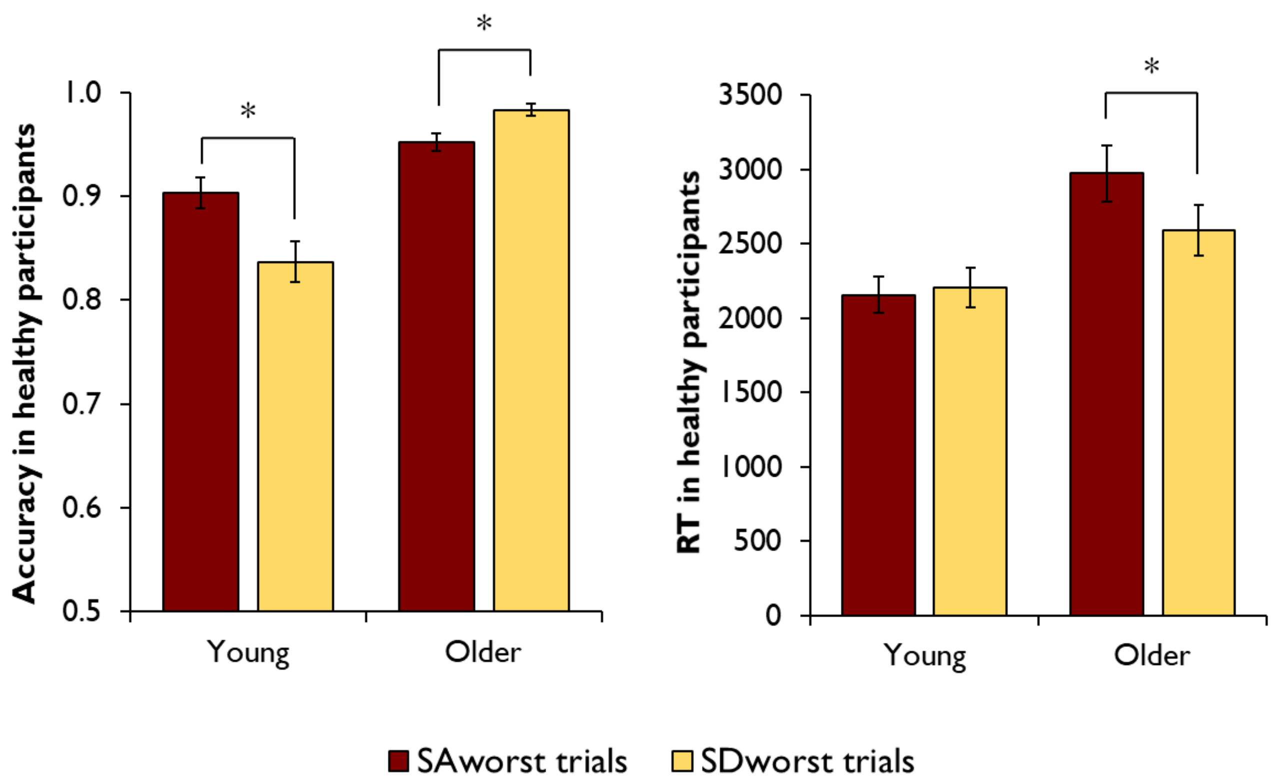
	All			Young			Older		
	B	s.e.	*p*	B	s.e.	*p*	B	s.e.	*p*
SD scores	-225	61.7	<0.001	-300	60.9	<0.001	-147	87.2	0.095
SA scores	-298	63.8	<0.001	-205	63.1	0.002	-391	91.3	<0.001
Group	332	105	0.002	----			----		
Group * SD scores	81.2	42.2	0.056	----			----		
Group * SA scores	-88.3	45.4	0.053	----			----		

*Figure 4: Modelled effects of patient scores on accuracy and RT. * indicates a significant interaction between variable and group ($p < 0.05$). ~ indicates $p < 0.06$.*



As an additional illustration of these effects, we analysed performance on subsets of trials on which one group of patients performed substantially better than the other. The results are shown in Figure 5. Young people were least accurate on the trials which SD patients found disproportionately difficult (SDworst), while older people produced fewer on the trials which SA patients found more difficult (SAworst). This difference was supported by a significant interaction between group and trial subset in a 2 x 2 mixed effect analysis (χ^2 = 7.33, p = 0.007). For RT, older people were significantly slower to respond to the SAworst trials, compared with the SDworst trials, while there were no difference between these trial sets in young people. Again, the difference between the groups was supported by a significant 2 x 2 interaction in a mixed effects analysis (χ^2 = 4.79, p = 0.029). These results support that the conclusion that older people's performance resembled that of SA patients with impaired semantic control processes, whereas the responses of young people were more similar to those of SD patients with impoverished semantic representations.

Figure 5: Performance on young and older people on trials for which SD or SA patients performed particularly poorly



Discussion

Effective semantic cognition relies on a store of knowledge representations as well as on control processes that regulate goal-directed retrieval and manipulation of this information. We investigated the status of these capacities in young and older adults by identifying the factors that influenced their performance on a synonym-matching verbal comprehension task. Young people had difficulty processing the meanings of low frequency and abstract words, whereas these factors had less influence on the performance of older people. This indicates that the young group had smaller and less detailed repositories of semantic knowledge, as suggested by a number of previous studies (Grady, 2012; Nilsson, 2003; Nyberg et al., 1996; Park et al., 2002; Rönnlund et al., 2005; Salthouse, 2004). In contrast, older people were strongly influenced by the balance of target vs. distractor semantic relationships (TDS), performing poorly on trials where the target semantic relationship was weak relative to irrelevant relationships present in the trial. This factor had less effect in the young group, suggesting that young people are more effective at engaging semantic control processes to identify task-relevant semantic information. This picture was supported by a second analysis, in which the performance of older people was best predicted by the scores of SA patients, who had established semantic control deficits. Conversely, the performance of the young group was more closely aligned with that of SD patients suffering from deterioration in knowledge representations. Taken together, these findings suggest a more nuanced picture of semantic cognition in later life than has been typically assumed in the past, with more detailed knowledge representations offset by weakness in controlled processing of this knowledge. We consider the implications for each age group in turn.

The performance of young people was best predicted by that of SD patients and, like SD patients, young people had particular difficulty on trials that probed the meanings of low frequency and abstract words. What is the interpretation of these findings? The suggestion is not, of course, that young people are suffering from some sort of neurodegeneration akin to that observed in SD. Rather, the most likely explanation is that they have under-developed semantic representations, the consequences of which resemble the disease-based weakening of semantic knowledge in SD. Indeed, it has often been observed that the trajectory of knowledge deterioration in SD is a mirror image of the acquisition of semantic knowledge in early development (Rogers & McClelland, 2004) and the present findings are an example of this phenomenon.

In SD, the meanings of low frequency words are thought to be particularly vulnerable to the disease process because they are represented more weakly in the knowledge store to begin with (Plaut, McClelland, Seidenberg, & Patterson, 1996; Rogers & McClelland, 2004). The semantic system has less opportunity to develop robust representations of the meanings of low frequency words because, by definition, it is exposed to them less often. This also explains why understanding of low frequency words tends to be acquired later in life (Kuperman, Stadthagen-Gonzalez, & Brysbaert, 2012; Morrison, Chappell, & Ellis, 1997; Stadthagen-Gonzalez & Davis, 2006). These same factors mean that the young adults in the present study (aged between 18 and 22) were yet to develop strong semantic representations for lower frequency words and hence showed strong effects of this variable. It is important, however, to note that young people showed strong effects of frequency in RT as well as accuracy (whereas older people showed neither). In other words, even when participants had sufficient knowledge of low frequency words to provide a correct response, they were still slower to do so. This suggests that young people's semantic representations for low frequency words, where they do exist, are less developed than those of older people. This result is also a mirror image of semantic degradation in SD, in which concepts are not lost in all-or-nothing fashion but gradually lose detail and acuity over time (Rogers et al., 2004). It is also consistent with a recent study reported by Pexman and Yap (in press), in which participants with lower vocabulary scores showed larger frequency effects on RT when making semantic decisions.

Imageability also had a larger effect on the accuracy of young people, with this group, but not the older participants, showing poorer knowledge of more abstract words. These results also align with the pattern seen in SD. The status of imageability effects in SD is a contentious issue, with some researchers claiming that patients have *more* intact knowledge of abstract words (Bonner et al., 2009; Cousins, York, Bauer, & Grossman, 2016; Yi, Moore, & Grossman, 2007). However, on the test used in the present study, SD patients reliably show large decrements in knowledge for more abstract words (Hoffman, 2016; Hoffman & Lambon Ralph, 2011; Jefferies et al., 2009). The most likely explanation for these findings is that more concrete words develop richer semantic representations because they are associated with a wide array of sensory-motor information (Paivio, 1986). This richer representation affords them some protection from the deterioration of knowledge in SD (Hoffman, McClelland, & Lambon Ralph, submitted). It is likely that this sensory richness also affects the ease of acquiring semantic representations during development (Kuperman et al., 2012; Morrison et al., 1997; Stadthagen-Gonzalez & Davis, 2006). As a consequence, young adults have less detailed representations of the meanings of abstract words.

In contrast to the findings already discussed, older people showed no effect of word frequency and weaker effects of imageability. These results suggest, in line with much previous work (Grady, 2012; Nilsson, 2003; Nyberg et al., 1996; Park et al., 2002; Rönnlund et al., 2005; Salthouse, 2004), that older people have broader and more detailed repositories of semantic knowledge, and consequently these factors have less influence on their performance. The scores of SD patients were also a much weaker predictor of performance in this group, suggesting that healthy ageing does not involve any loss of semantic knowledge of the kind seen in SD. This conclusion is consistent with data on the neuroanatomical correlates of SD and the effects of healthy ageing on cortical volumes. Knowledge loss in SD is strongly linked to atrophy of the ventral anterior temporal cortex (Butler et al., 2009; Mion et al., 2010). However, this region exhibits little age-related volume loss in healthy individuals, compared with other areas such as prefrontal cortex (Fjell et al., 2009). Indeed, a recent study in 556 healthy older adults found that volume of the ventral temporal cortices was a positive predictor of an individual's quantity of semantic knowledge (Hoffman et al., 2017). However, this association was entirely mediated by educational level and childhood IQ, suggesting that this was a lifelong association rather than an effect of the ageing process.

The present study has, however, identified other factors that have a greater influence on semantic processing in old age. Older people showed much stronger effects of the target vs. distractor strength (TDS), a measure of the strength of the target semantic relationship on each trial relative to irrelevant distractor relationships. Older people were slower and less accurate to respond when the target semantic relationship was weak and competition from irrelevant semantic relationships was strong. Identifying the correct response under these conditions places high demands on semantic control processes that regulate the activation of semantic knowledge (Badre & Wagner, 2007; Lambon Ralph et al., 2017; Thompson-Schill, 2003). These results therefore indicate that older people are less able to exercise semantic control. In line with this view, performance in this group was most strongly predicted by the scores of patients with SA, a group characterised by semantic control deficits (Jefferies & Lambon Ralph, 2006). Older adults were also less accurate when making decisions about words with high semantic diversity (although this effect fell just short of conventional significance levels). Similarly, SA patients have difficulty in processing these words because of their intrinsically complex and contextually-varying meanings (Hoffman et al., 2011b).

Although an old-age deficit in semantic control has not been reported previously, it is consistent with our understanding of changes in neural structure and function in later life. Semantic control is underpinned by a network of regions including inferior parietal, posterior temporal and, most prominently, inferior prefrontal cortex (Jefferies, 2013; Noonan et al., 2013; Vatansever et al., 2017). Inferior prefrontal cortex shows large age-related declines in volume in later life (Fjell et al., 2009; Raz et al., 1997; Raz et al., 2005) and changes in functional activation are also frequently observed in this region (Cabeza, 2002; Grady, 2012). Indeed, a recent neuroimaging meta-analysis indicates that older people show reduced activation during semantic processing in inferior prefrontal cortex, as well as other regions associated with semantic control (Hoffman & Morcom, 2017). These findings suggest a possible neural mechanism for the behavioural effects observed in the present study. Of course, much more work would be needed to link these behavioural and neural observations more directly and to delineate the precise circumstances under which reductions in prefrontal activity have measurable impacts on semantic performance. However, the age-related increases in effects of target vs. distractor strength observed in the present study suggest that conditions of high semantic competition are an area of particular weakness in later life.

References

Almaghyuli, A., Thompson, H., Lambon Ralph, M. A., & Jefferies, E. (2012). Deficits of semantic control produce absent or reverse frequency effects in comprehension: evidence from neuropsychology and dual task methodology. *Neuropsychologia, 50*(8), 1968-1979. doi:10.1016/j.neuropsychologia.2012.04.022

Baayen, R. H., Piepenbrock, R., & van Rijn, H. (1993). *The CELEX lexical database (CD-ROM)*. Philadelphia, PA: Linguistic Data Consortium, University of Pennsylvania.

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

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255-278.

Bonner, M. F., Vesely, L., Price, C., Anderson, C., Richmond, L., Farag, C., . . . Grossman, M. (2009). Reversal of the concreteness effect in semantic dementia. *Cognitive Neuropsychology, 26*, 568-579.

Butler, C. R., Brambati, S. M., Miller, B. L., & Gorno-Tempini, M. L. (2009). The Neural Correlates of Verbal and Nonverbal Semantic Processing Deficits in Neurodegenerative Disease. *Cognitive and Behavioral Neurology, 22*(2), 73-80.

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychol Aging, 17*(1), 85.

Coltheart, M. (1981). The MRC Psycholinguistic Database. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 33*(Nov), 497-505.

Cousins, K. A., York, C., Bauer, L., & Grossman, M. (2016). Cognitive and anatomic double dissociation in the representation of concrete and abstract words in semantic variant and behavioral variant frontotemporal degeneration. *Neuropsychologia, 84*, 244-251.

Crutch, S. J., & Warrington, E. K. (2008). Contrasting patterns of comprehension for superordinate, basic-level, and subordinate names in semantic dementia and aphasic stroke patients. *Cognitive Neuropsychology, 25*(4), 582-600.

Fjell, A. M., Westlye, L. T., Amlien, I., Espeseth, T., Reinvang, I., Raz, N., . . . Fischl, B. (2009). High consistency of regional cortical thinning in aging across multiple samples. *Cerebral Cortex*, bhn232.

Funnell, E. (1995). Objects and properties: A study of the breakdown of semantic memory. *Memory, 3*(3-4), 497-518.

Gloor, P. (1997). *The temporal lobe and the limbic system*. Oxford: Oxford University Press.

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

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.

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

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., Jefferies, E., & Lambon Ralph, M. A. (2010). Ventrolateral prefrontal cortex plays an executive regulation role in comprehension of abstract words: convergent neuropsychological and repetitive TMS evidence. *Journal of Neuroscience, 30*(46), 15450-15456. doi:10.1523/JNEUROSCI.3783-10.2010

Hoffman, P., Jefferies, E., & Lambon Ralph, M. A. (2011a). Remembering 'zeal' but not 'thing': reverse frequency effects as a consequence of deregulated semantic processing. *Neuropsychologia, 49*(3), 580-584. doi:10.1016/j.neuropsychologia.2010.12.036

Hoffman, P., Jones, R. W., & Lambon Ralph, M. A. (2012). The degraded concept representation system in semantic dementia: damage to pan-modal hub, then visual spoke. *Brain, 135*(Pt 12), 3770-3780. doi:10.1093/brain/aws282

Hoffman, P., & Lambon Ralph, M. A. (2011). Reverse concreteness effects are not a typical feature of semantic dementia: Evidence for the hub-and-spoke model of conceptual representation. *Cerebral Cortex, 21*, 2103-2112.

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., McClelland, J. L., & Lambon Ralph, M. A. (submitted). Concepts, control and context: A connectionist account of normal and disordered semantic cognition.

Hoffman, P., & Morcom, A. M. (2017). Age-related changes in the neural networks supporting semantic cognition: A meta-analysis of 47 functional neuroimaging studies. *bioRxiv*, 167064. doi:https://doi.org/10.1101/167064

Hoffman, P., Rogers, T. T., & Lambon Ralph, M. A. (2011b). 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.

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.

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

Jefferies, E., Patterson, K., Jones, R. W., & Lambon Ralph, M. A. (2009). Comprehension of concrete and abstract words in semantic dementia. *Neuropsychology, 23*, 492-499.

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

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.

Mayberry, E. J., Sage, K., & Lambon Ralph, M. A. (2011). At the edge of semantic space: The breakdown of coherent concepts in semantic dementia is constrained by typicality and severity but not modality. *Journal of Cognitive Neuroscience, 23*(9), 2240-2251.

Mikolov, T., Chen, K., Corrado, G., & Dean, J. (2013). Efficient estimation of word representations in vector space. *arXiv preprint arXiv:1301.3781*.

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

Morrison, C. M., Chappell, T. D., & Ellis, A. W. (1997). Age of Acquisition Norms for a Large Set of Object Names and Their Relation to Adult Estimates and Other Variables. *The Quarterly Journal of Experimental Psychology Section A, 50*(3), 528-559. doi:10.1080/027249897392017

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

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.

Paivio, A. (1986). *Mental representations: A dual-coding approach*. Oxford: Oxford University Press.

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.

Pereira, F., Gershman, S., Ritter, S., & Botvinick, M. (2016). A comparative evaluation of off-the-shelf distributed semantic representations for modelling behavioural data. *Cognitive Neuropsychology, 33*(3-4), 175-190.

Pexman, P. M., & Yap, M. J. (in press). Individual Differences in Semantic Processing: Insights from the Calgary Semantic Decision Project. *Journal of Experimental Psychology: Learning, Memory, & Cognition*.

Plaut, D. C., McClelland, J. L., Seidenberg, M. S., & Patterson, K. (1996). Understanding normal and impaired word reading: Computational principles in quasi-regular domains. *Psychological Review, 103*(1), 56-115.

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.

Raz, N., Gunning, F. M., Head, D., Dupuis, J. H., McQuain, J., Briggs, S. D., . . . Acker, J. D. (1997). Selective aging of the human cerebral cortex observed in vivo: differential vulnerability of the prefrontal gray matter. *Cerebral cortex (New York, NY: 1991), 7*(3), 268-282.

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., . . . Acker, J. D. (2005). Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cerebral Cortex, 15*(11), 1676-1689.

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

Rogers, T. T., Hocking, J., Noppeney, U., Mechelli, A., Gorno-Tempini, M. L., Patterson, K., & Price, C. J. (2006). Anterior temporal cortex and semantic memory: reconciling findings from neuropsychology and functional imaging. *Cognitive, Affective, & Behavioral Neuroscience, 6*(3), 201-213.

Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., & Patterson, K. (2004). Structure and deterioration of semantic memory: A neuropsychological and computational investigation. *Psychological Review, 111*(1), 205-235.

Rogers, T. T., & McClelland, J. L. (2004). *Semantic cognition: A parallel distributed processing approach*. Cambridge, MA: MIT Press.

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. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review, 103*(3), 403.

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

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

Stadthagen-Gonzalez, H., & Davis, C. J. (2006). The Bristol norms for age of acquisition, imageability, and familiarity. *Behavior Research Methods, 38*(4), 598-605.

Thompson-Schill, S. L. (2003). Neuroimaging studies of semantic memory: inferring "how" from "where". *Neuropsychologia, 41*(3), 280-292.

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.

Vatansever, D., Bzdok, D., Wang, H.-T., Mollo, G., Sormaz, M., Murphy, C., . . . Jefferies, E. (2017). Varieties of semantic cognition revealed through simultaneous decomposition of intrinsic brain connectivity and behaviour. *Neuroimage*.

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.

Visser, M., Jefferies, E., & Lambon Ralph, M. A. (2010). Semantic processing in the anterior temporal lobes: A meta-analysis of the functional neuroimaging literature. *Journal of Cognitive Neuroscience, 22*, 1083-1094.

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

Woollams, A. M., Cooper-Pye, E., Hodges, J. R., & Patterson, K. (2008). Anomia: A doubly typical signature of semantic dementia. *Neuropsychologia, 46*, 2503-2514.

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

Yi, H. A., Moore, P., & Grossman, M. (2007). Reversal of the concreteness effect for verbs in patients with semantic dementia. *Neuropsychology, 21*(1), 9-19.