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How do we understand the age-related increase in semantic priming?

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Outline

Background

- Brain changes in normal ageing
- Compensatory mechanisms

Semantic priming

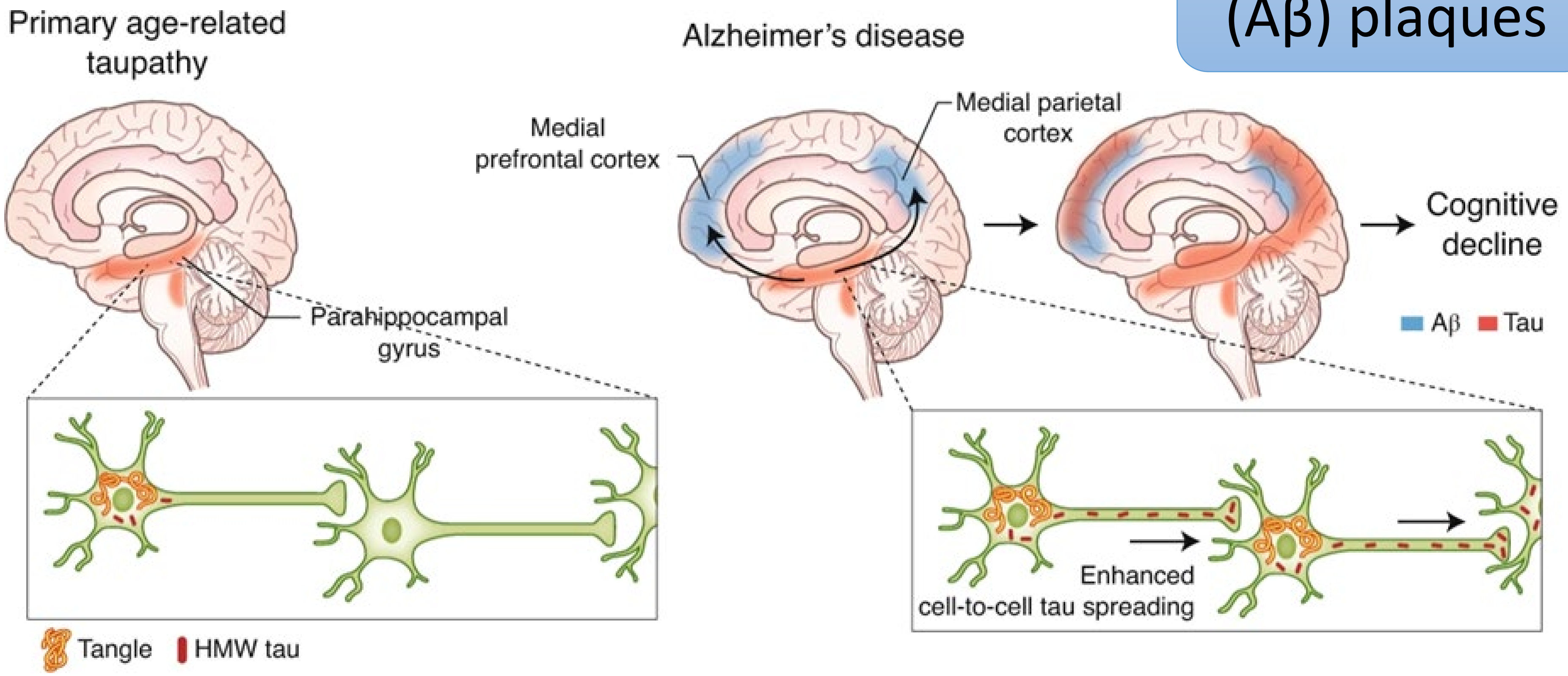
- Why semantic priming?
- Experimental design
- Preliminary findings

Background

Common signs of neurodegeneration

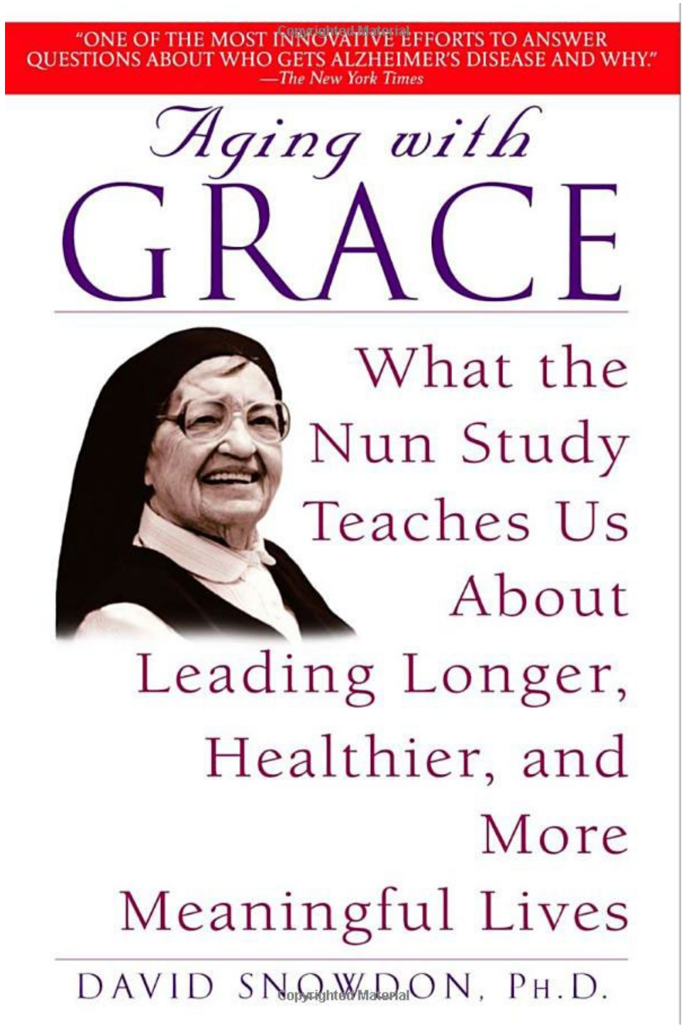
β-amyloid (Aβ) plaques

tau-containing neurofibrillary tangles



Busche & Hyman (2020). Synergy between amyloid-*β* and tau in Alzheimer's disease. *Nature Neuroscience*.

The Nun Study



"One astounding finding from the Nun Study came from comparing language usage in their youth with the development of AD later in life. In brief, this type of analysis convincingly demonstrated that complex cognitive skills and abilities at a relatively young age correlate with a *decreased* likelihood of developing AD in late adulthood."

--- Sweatt et al., 2010

What is normal in normal aging? Effects of aging, amyloid and Alzheimer's disease on the cerebral cortex and the hippocampus

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ABSTRACT

What can be expected in normal aging, and where does normal aging stop and pathological neurodegeneration begin? With the slow progression of age-related dementias such as Alzheimer's disease (AD), it is difficult to distinguish age-related changes from effects of undetected disease. We review recent research on changes of the cerebral cortex and the hippocampus in aging and the borders between normal aging and AD. We argue that prominent cortical reductions are evident in fronto-temporal regions in elderly even with low probability of AD, including regions overlapping the default mode network. Importantly, these regions show high levels of amyloid deposition in AD, and are both structurally and functionally vulnerable early in the disease. This *normalcy-pathology homology* is critical to understand, since aging itself is the major risk factor for sporadic AD. Thus, rather than necessarily reflecting early signs of disease, these changes may be part of normal aging, and may inform on why the aging brain is so much more susceptible to AD than is the younger brain. We suggest that regions characterized by a high degree of life-long plasticity are vulnerable to detrimental effects of normal aging, and that this age-vulnerability renders them more susceptible to additional, pathological AD-related changes. We conclude that it will be difficult to understand AD without understanding why it preferably affects older brains, and that we need a model that accounts for age-related changes in AD-vulnerable regions independently of AD-pathology.

Modifiable risk factors

Comorbidities

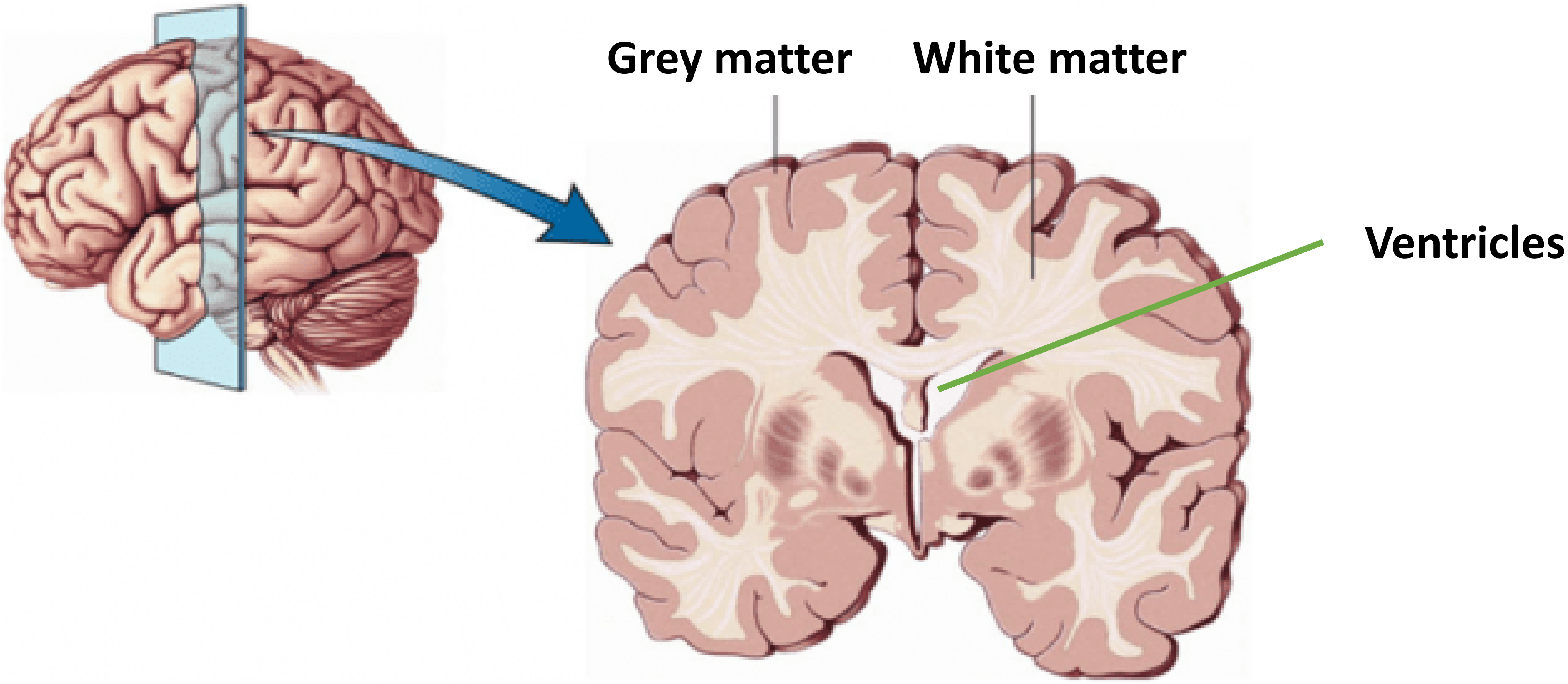
- Vascular diseases
- Type II diabetes
- Traumatic brain injury
- Epilepsy
- Depression

Lifestyle

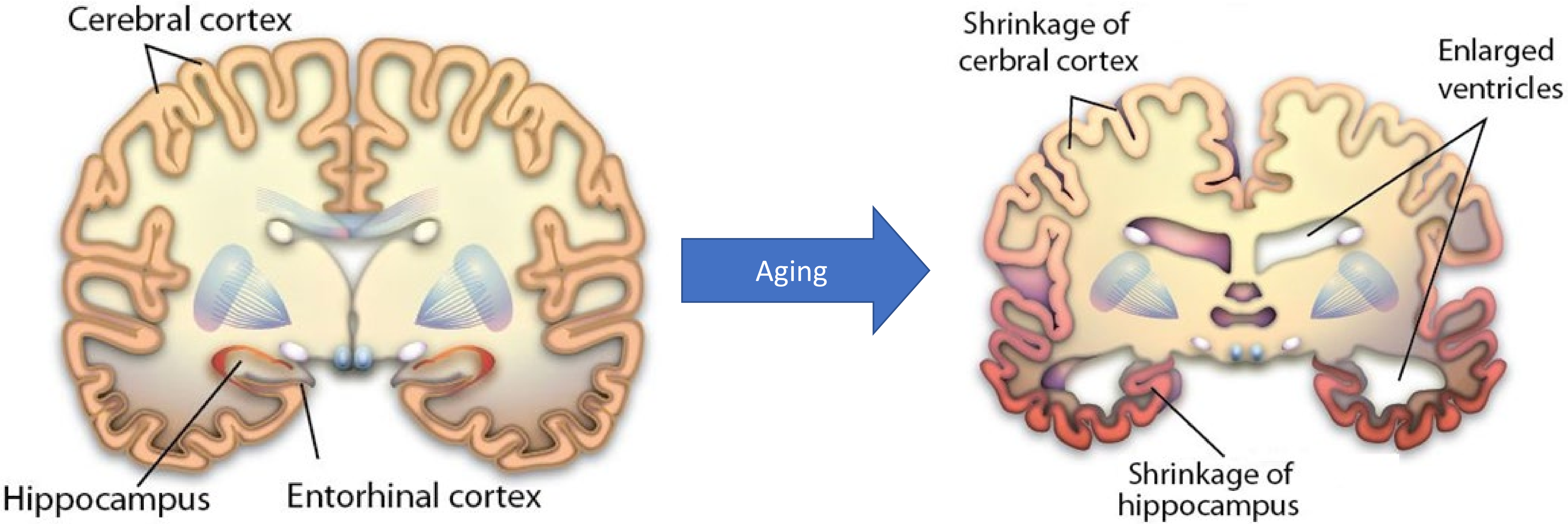
- Physical activity
- Sleep Disturbance
- Diet
- Smoking
- Alcohol

Edwards III et al. (2019). Modifiable risk factors for Alzheimer's disease. *Frontiers in Aging Neuroscience*, *11*, 146.

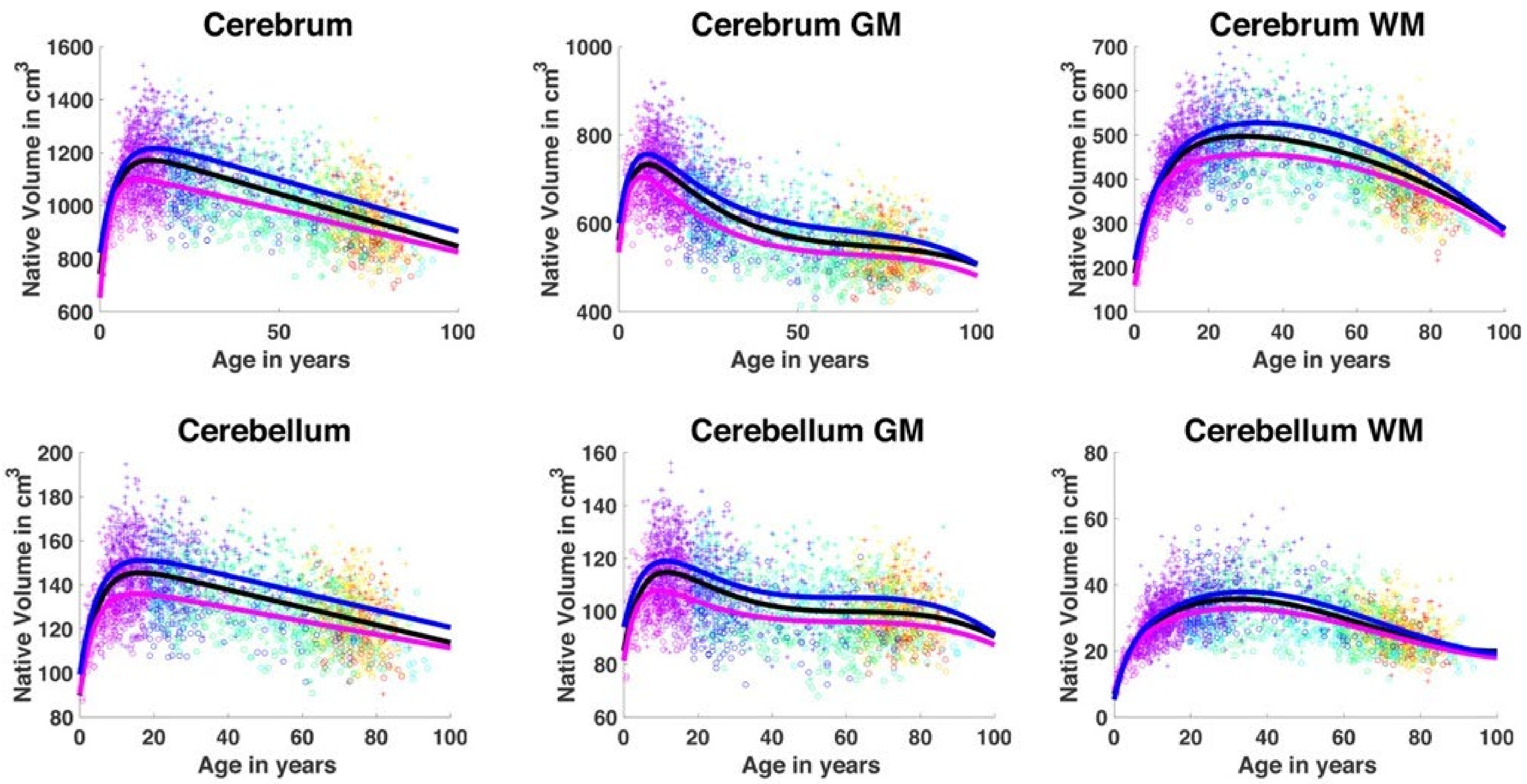
Grey matter, white matter, & ventricles



Young vs. AGING brain



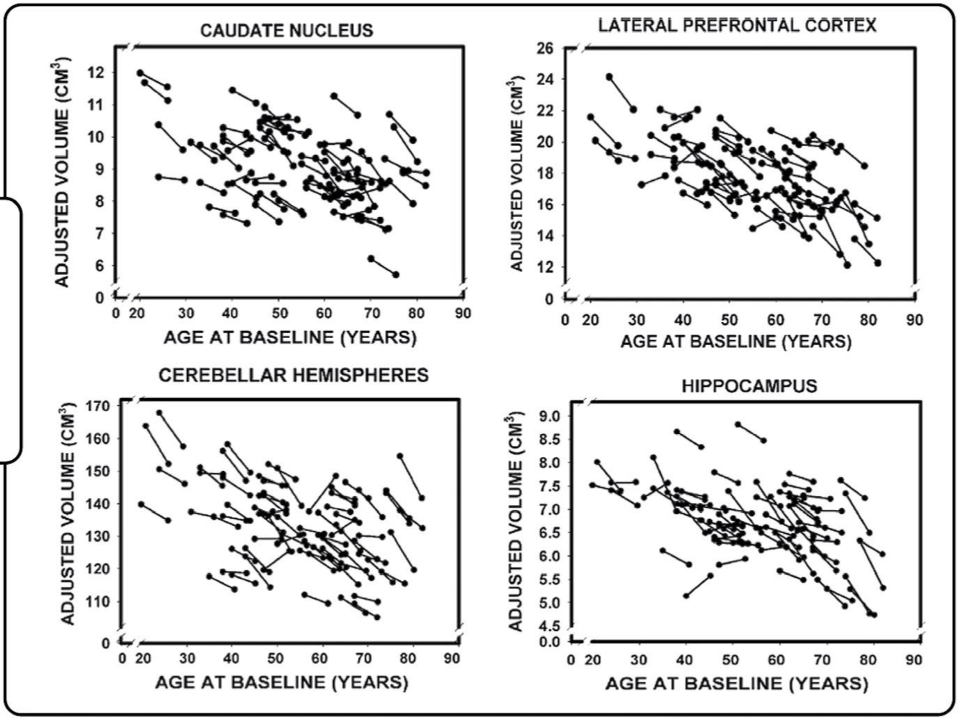
Structural hallmarks of brain aging



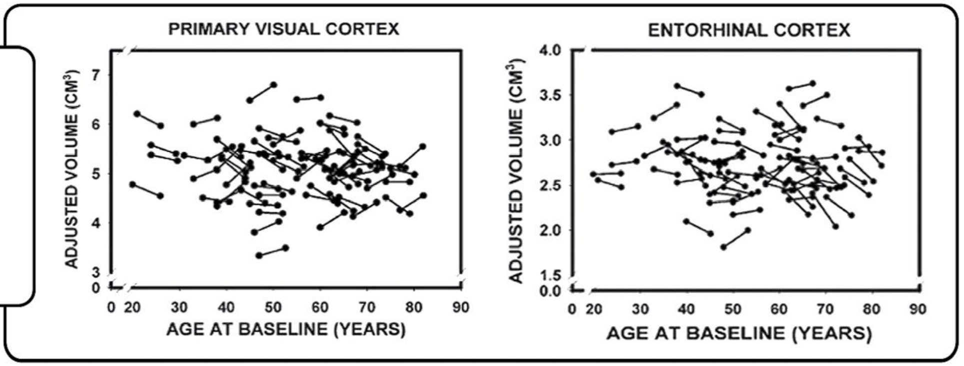
Coupé et al. (2017). *Human brain mapping*.
Towards a unified analysis of brain maturation and aging across the entire lifespan.

Differential changes in ageing

Brain regions that reduce in volume with age.

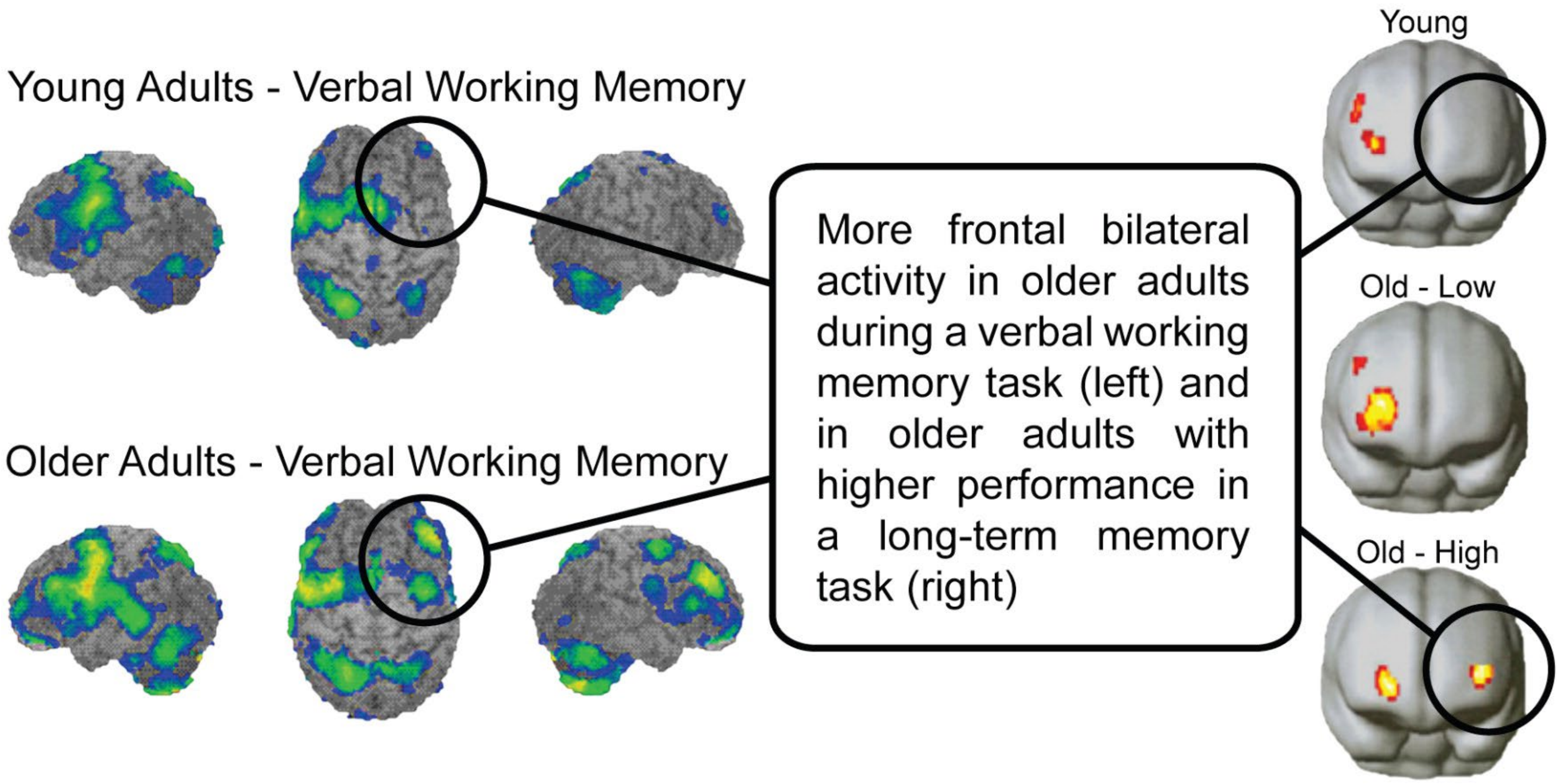


Brain regions with minimal reduction or stable volume with age.



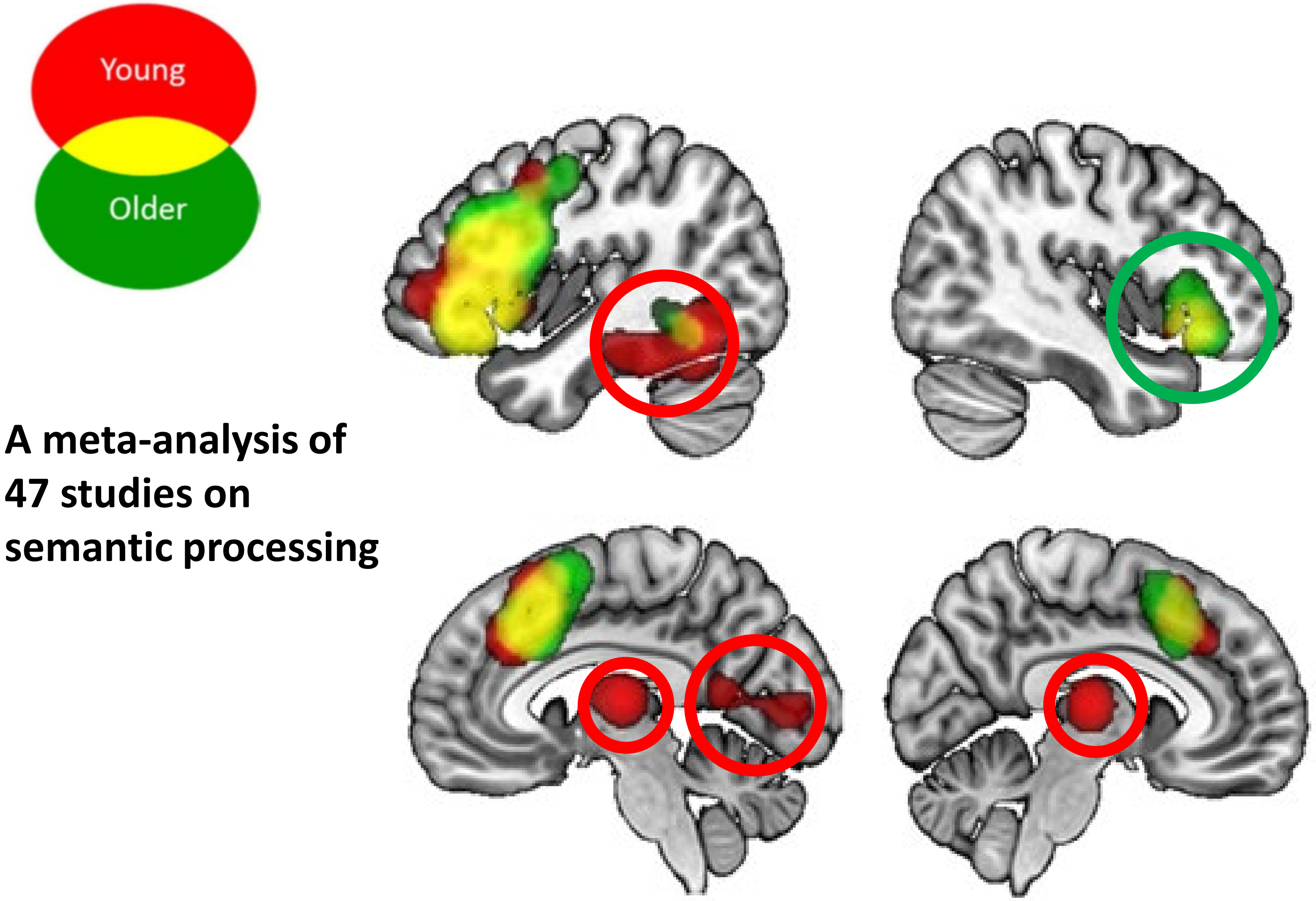
Park & Reuter-Lorenz (2009). *Annual Review of Psychology*.

Age-related neural reorganization



Cabeza (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*.

Compensation mechanisms in older adults



A meta-analysis of 47 studies on semantic processing

Both groups: activated a broad network of left-lateralized regions.

Younger adults: distinct activation pattern in the left temporoparietal regions at the back of the brain and in the bilateral thalamus.

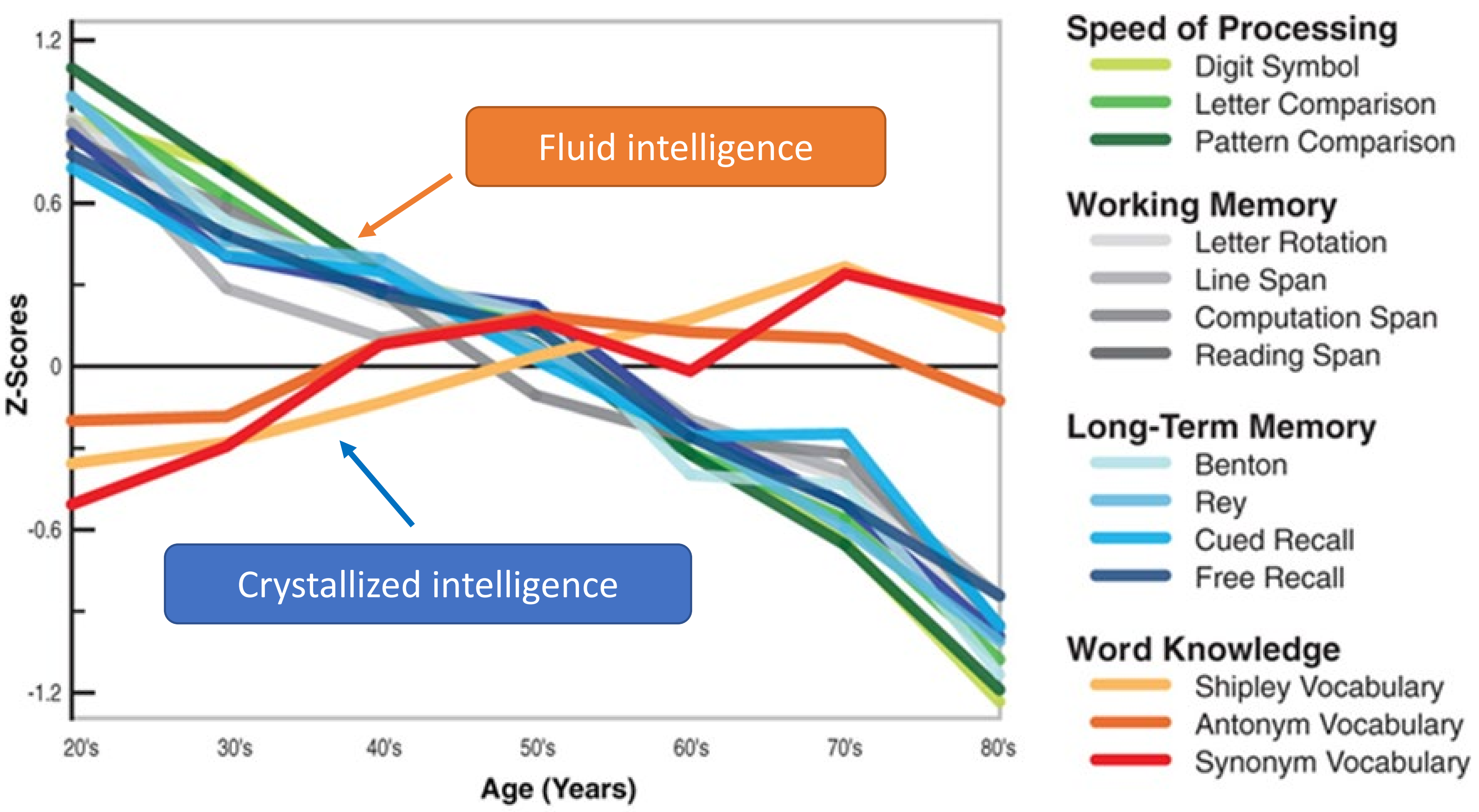
Older adults: more activation in the right frontal regions. Activity increases with semantic performance → **COMPENSATION**

Hoffman & Morcom (2018). *Neuroscience & Biobehavioral Review*.

Middle age: an understudied life stage

- Most neuroscientific studies on cognitive ageing typically only compare **younger** and **older** adult groups.
  - The difficulty here is probably pragmatic than theoretical—it is simply too time-consuming and costly for middle-aged adults around the world to spend a few hours or days to take part in a research program.
  - We still know so little about the brain changes in the middle age.

Age-related cognitive changes



Park & Bishop (2013). *Dialogues in Clinical Neuroscience*.

Importance of crystallized intelligence

- **Crystallized intelligence may have a compensatory effect on cognition in old age**
  - Default–Executive Coupling Hypothesis of Aging (DECHA; Spreng et al., 2018)
  - "Semanticization of cognition"

- **Because crystallized intelligence is often the last to decline in dementia, generally it has received relatively less attention.**
  - For instance, traditional screening tools for dementia included a few items on crystallized intelligence, based on
    - Picture naming tests
    - Categorization tasks (apples and bananas).
    - Verbal fluency (single category).

Cases of category-specific impairments

Cases	Preserved	Impaired	Modality
C.H.C. (Nielson, 1946)	Living things (including flowers)	Inanimate objects and food	Sight or touch
Flora D (Nielson, 1946)	Inanimate objects	Animate objects	Not specified
3 patients with diffuse cerebral lesions (Warrington, 1975)	Superordinate categories	Subordinate items	Verbal
4 patients (Warrington & Shallice, 1984)	Inanimate objects	Living things & foods	Both visual and verbal
1 patient (Warrington & Shallice, 1984)	Abstract words	Concrete words	Verbal

Warrington (1975)

- In dementia, when given probe questions about each item (animals, household objects, and birds were used as test items),
  - patients were unable to make judgments requiring detailed knowledge of each concept (“Is this a foreign animal?“)
  - performed much better when asked to determine the general (superordinate) category (“Is this an object or an animal?“).

Semantic memory disturbance in AD patients

- **Prominent naming disorder (Chertkow, Bub, & Seidenberg, 1989)**
  - Semantic deficits may be the primary cause of anomia in early AD.
    - Semantic errors are much more frequent on object-naming tasks than mere perceptual misrecognitions (Martin & Fedio, 1983)
    - The anomia of mild to moderate AD patients were more closely associated with a semantic deficit (impaired category fluency) than perceptual deficit (form discrimination task) (Huff, Corkin, & Growdon, 1986)
    - Demented patients showing very disturbed comprehension and naming of objects could still perform within normal limits on a variety of perceptual tests.

Semantic memory disturbance in AD patients

- Decreased word fluency (Grant & Adams, 1986)
- Impaired ranking of semantic attributes (Grober, Buscke, Kawas, & Fuld, 1985)
- Altered patterns of paradigmatic word associations (Gewirth, Shindler, and Hier, 1984)
- Huff et al. (1986) demonstrated a definite item-to-item correspondence between loss of word comprehension and anomia for a particular concept in AD patients.

Intermediate summary

- Present screening tools for dementia and mild cognitive impairment may have undervalued the contributions of semantics to our overall cognitive functions.

- Instead of making the assumption that semantic functions are relatively intact in old age, it is a worthwhile effort to examine the associations of individual differences in semantic functions.

- In particular, from the compensation point of view, would increasing the crystallized knowledge be a viable lifestyle intervention for combatting dementia?

Semantic priming

Semantic memory & mental lexicon

- **Semantic memory**: the system which processes, stores, and retrieves information about the meaning of words, objects/concepts, and facts (Tulving, 1972).

- **Mental lexicon**: The complete list of vocabulary of an individual.

"okra pods" 秋葵

Damasio's view on semantic representations (1989)

"The representations of physical structure components of entities are recorded in the same neural ensembles in which corresponding activity occurred during perception, but the combinatorial arrangements which describe their pertinent linkages … are stored in separate neural ensembles called convergence zones."

"The concerted reactivation of physical structure fragments, on which recall of experiences depends, requires the firing of convergence zones and the concomitant firing of the feedback projections arising from them."

"Convergence zones are located throughout the telencephalon, at multiple neural levels, in association cortices of different orders, limbic cortices, subcortical limbic nuclei, and non-limbic subcortical nuclei such as the basal ganglia."

Damasio. 1989. *Cognition*.

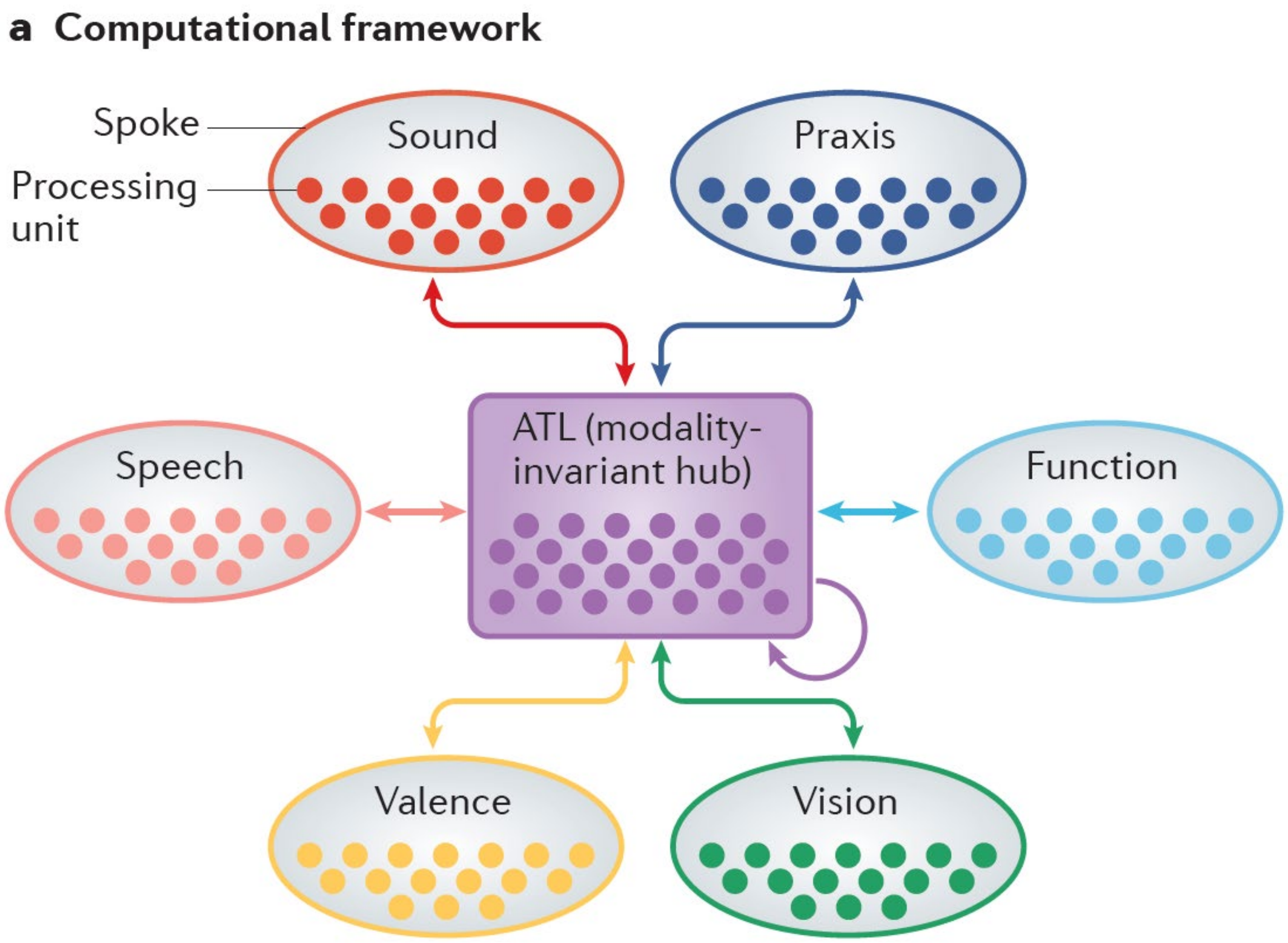
What do category-specific impairments tell us?

"The analysis of neuropsychological disorders of lexical processing has provided important clues about the general organization of the lexical system and the internal structure of the processing components.

Reports of patients with selective dysfunction of specific semantic categories such as abstract versus concrete words, living things versus inanimate objects, animals, fruits and vegetables, proper names, and so forth, support the hypothesis that ***the neural organization of the semantic processing component is organized in these categories.****"*

Caramazza & Hillis. 1991. *Nature.*

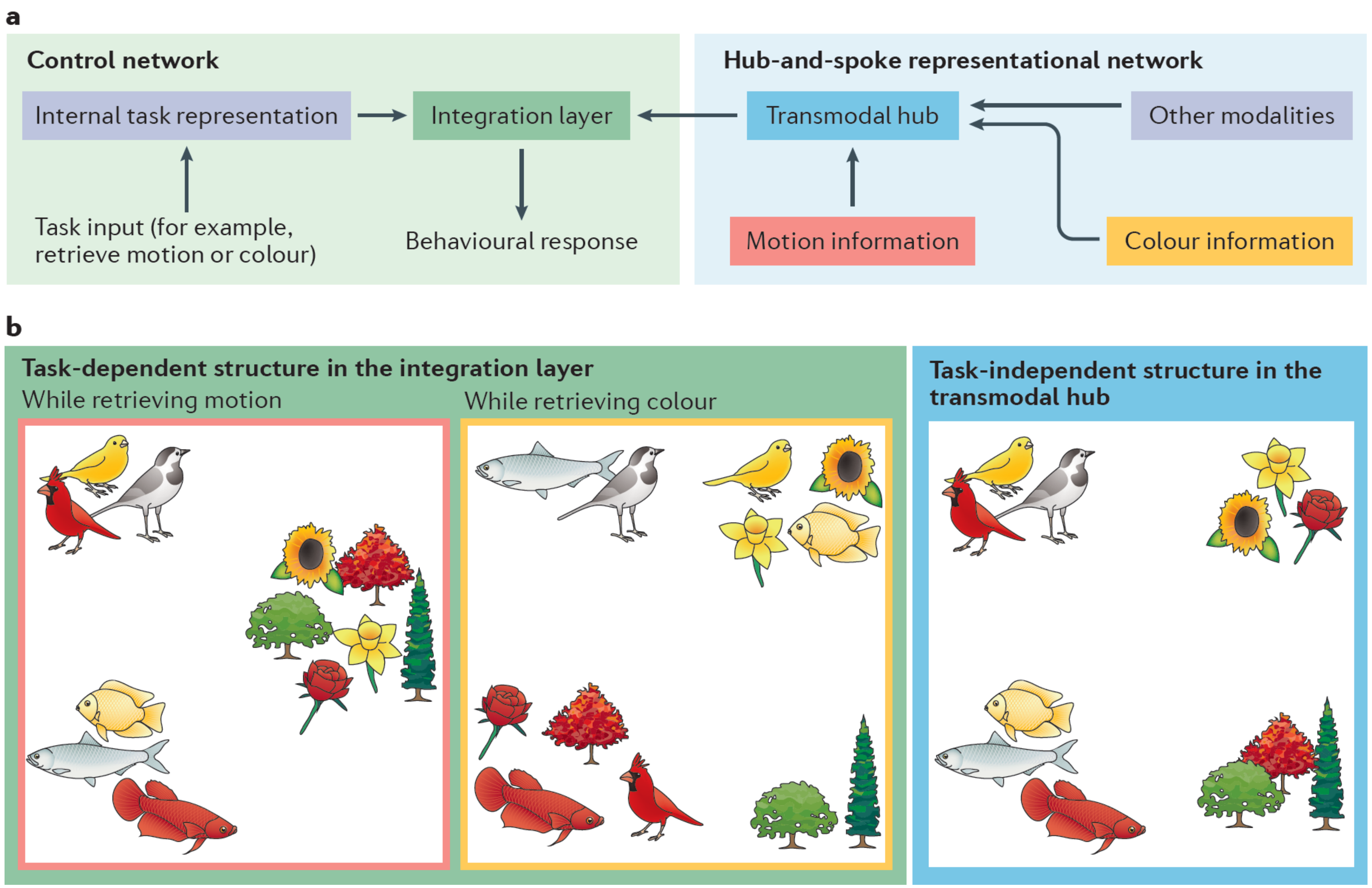
Anterior temporal lobe & "hub-and-spoke" theory



"Conceptual knowledge might arise through learning about the statistical structure of our multimodal experiences"

Patterson et al. 2007. *Nat Rev Neurosci.;* Lambon Ralph et al. 2017. *Nat Rev Neurosci.*

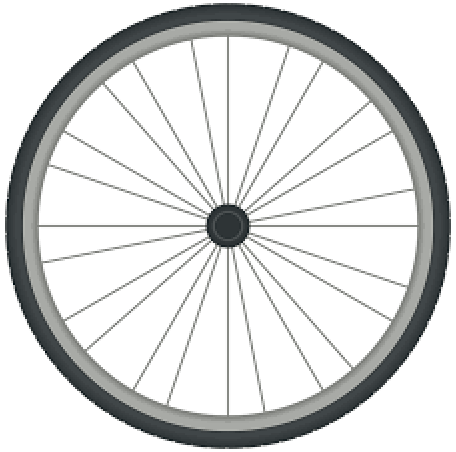
Controlled semantic cognition (CSC) theory

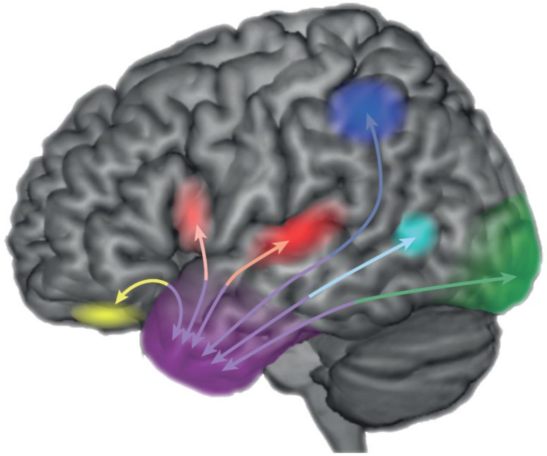


Lambon Ralph et al. 2017. *Nat Rev Neurosci*.

Theoretical development

1971	Dual coding theory	Paivio
1972	Semantic vs. episodic memory	Tulving
1989	Convergence zone	Damasio
2005	Hub-and-spoke theory	Patterson et al.
2017	Controlled semantic cognition (CSC)	Lambon Ralph et al.





Semantic priming effect (SPE)

- **What is SPE?**
  - If the two semantically related words (i.e., within the same semantic category such as “tools” or associated, e.g., “monkey” and “banana”) are presented in succession, the processing of the 2nd word would be facilitated in a range of tasks, including lexical decision, naming, categorization, etc.

Importance of the priming paradigm

- Priming results are important for two main reasons.
  - Normal priming results can be found in patients who perform poorly on other semantic memory tests, enabling us to distinguish between
    - (1) loss of, or damage to, information in semantic memory;
    - (2) voluntary access to that information.
  - By charting the priming effects for different kinds of words / semantic relations, we can investigate the detailed pattern of loss and preservation of different types of semantic information.

Hyper-priming

- Refers to an increase in semantic priming effect in primed lexical decision task within pathological groups (Chertkow et al., 1989; Moss & Tyler, 1995)
- Compared to younger adults, in the visual domain, older adults have also been reported to exhibit hyper-priming.
- The finding is sometimes attributed to lower processing speed and poor inhibition in older adults.

3 competing hypotheses on hyper-priming

- **H1a**
  - **Hyper-priming**, i.e., the age-related increase in auditory semantic priming (ASP) effect, represents the **general growth in semantic knowledge with age**.
- **H1b**
  - Hyper-priming is **merely a by-product of lower RT of older adults**, which leaves more room for facilitation. In other words, the smaller priming effect in younger adults is caused by a ceiling effect.
- **H1c**
  - Hyper-priming is caused by the **reduced ability of older adults in inhibiting the unrelated prime**, which ***hinders target processing***.

Age-related differences in concreteness and relations

- **H2a**: Is there ***selective*** age-related differences in the neural representation of abstract words?
  - Is Group (young / middle-aged / old) × Concreteness (concrete / abstract) significant?
- **H2b**: Is there ***selective*** age-related differences in the neural representations of categorical vs. associative relations?
  - Is Group (young / old) × Relatedness (related / unrelated)?
- **H2c:** The semantic representations of ***concrete and abstract relations*** have ***dissociable developmental trajectories due to normal aging***.
  - Is the three-way interaction Group x Concreteness x Relation significant?
  - The priming effect for categorically related abstract pairs may be smallest for older adults.

Neural hypotheses

- **H3a**: The ***continued growth in semantic ability during middle age*** is accompanied by ***strengthened RSFCs in the left frontotemporal network, especially between DLPFC and ATL***.

- **H3b**: The ***decline in semantic ability during senescence*** is accompanied by ***weakened RSFCs in the left frontotemporal network, especially between DLPFC and ATL***.

Experimental protocol

Visit	Content	Purpose
1	Screening & questionnaire	General health & cognitive screening; To gather basic health info (e.g., blood pressure, pulse rate, BMI, vision, and audition) and language background
2	Cognitive battery	To assess the participants’ cognitive functions in various domains comprehensively
3	MRI	Semantic priming task + recognition test
4	EEG	Semantic priming task

Cognitive battery

Task	Task name	Cognitive measures
1	SSRT	Procedural memory
2	Stroop	Processing speed and inhibition
3	Digit Span	Phonological short term memory
4	Hong Kong List Learning Test Trial 1-3	Verbal short term memory
5	One-back	Attention
6	Hong Kong List Learning Test Trial 4 (10 min)	Delayed verbal memory (10 min)
7	Tower of Hanoi	Fluid intelligence and visuospatial reasoning
8	Hong Kong List Learning Test Trial 5 (30 min)	Delayed verbal memory (30 min)
9	Hong Kong List Learning Test – Recognition	Delayed recognition memory
10	Picture naming	Object recognition and semantic retrieval
11	Verbal fluency	Controlled semantic retrieval
12	Operation span	Working memory
13	Trail making A & B	Processing speed and visual search
14	SSRT retest	Procedural memory

Fong et al. 2020. *Quarterly Journal of Experimental Psychology*.
Fong et al. 2022. *Frontiers in Human Neuroscience*.

Rationale of the experiment

- The majority of the published research on semantic priming focused on the **visual** domain and have considered **relatedness** and **concreteness**.
- Some have additionally considered the distinction of **associative/thematic** and **categorical/taxonomic** relationship (e.g., Sachs et al., 2008; Chen et al., 2014)
  - However, the categorical relations are often confounded with associations (e.g., cats and dogs), and vice versa, casting doubts to the differential representations of the two relationships.
- In addition to explaining the **hyper-priming effect**, we would like to tease apart these two semantic dimensions, and additionally determine whether the **trajectory of ageing** is distinct for each type of **semantic relation (A/C/CA)** and **concreteness (concrete/abstract)**.

Hong Kong Cantonese Word Database

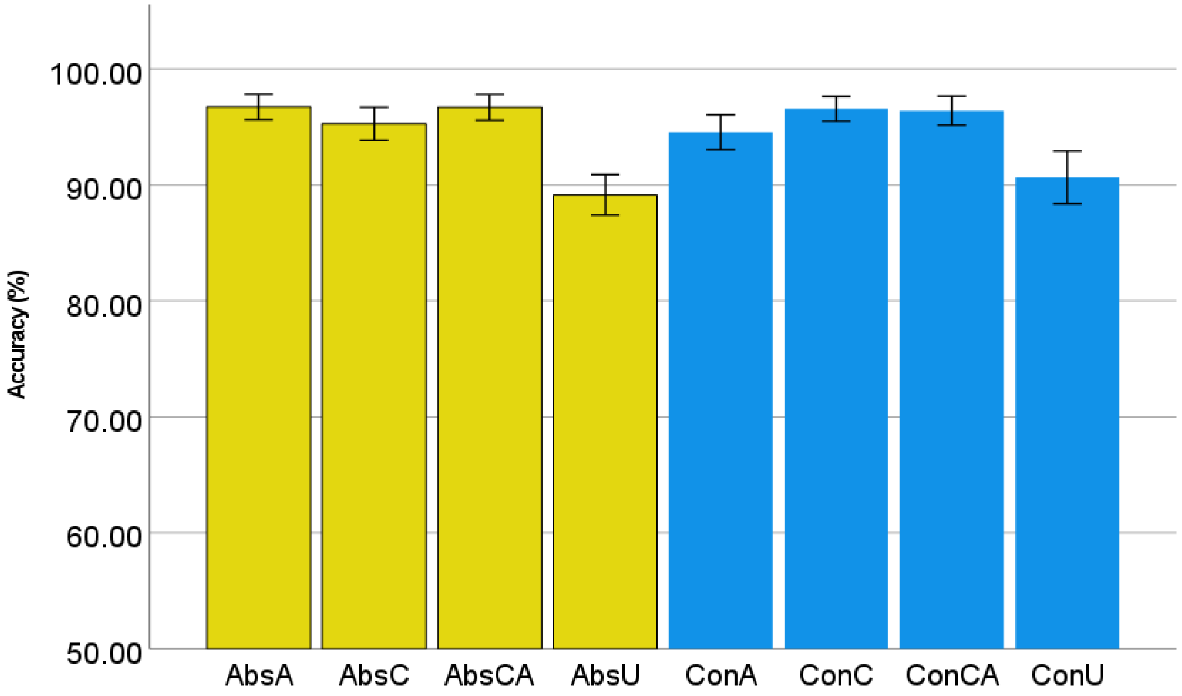
PairID	Word1	Word2	RelatednessY	RelatednessO	CategoricalnessY	CategoricalnessO	AssociativenessY	AssociativenessO	FamiliarityY1	FamiliarityO1	FamiliarityY2	FamiliarityO2	Concreteness1	Concreteness2
1	耐性	心機	3.9	3.8	4	4	4	4	4.56	4.06	4.38	3.88	1.79	1.47
2	信念	抱負	4.05	3.79	4	3.5	4	4	3.81	4.13	3.38	4.31	1.42	1.37
3	指引	介紹	3.6	3.52	3	3	4	3.5	4.31	3.94	4.44	3.88	2.26	2.32
4	人脈	關係	4.35	3.88	4	4	4	4.5	4	3.59	4.69	4.18	1.95	1.68
5	地位	身份	4.25	4.45	4	4	5	4.5	3.94	4.25	4	4.31	1.89	2
6	文憑	學歷	4.35	4.68	4	4	4.5	4.5	4	4.47	4.69	4.33	2.95	2.62
7	檔案	文件	4.5	4.54	5	4.5	5	4.5	4.25	4.38	4.38	4.44	3.37	3.32
8	武術	功夫	4.55	4.68	5	4.5	4.5	4.5	3.31	4.07	3.69	4	2.52	2.67
9	物理	化學	4.55	3.58	4	4	4	4.5	3.81	3.56	4.19	3.81	2.32	2.58
10	現實	理想	4.25	3.58	3	3	4	4	4.56	3.88	4.25	4.06	1.74	1.47
11	經濟	金融	4.6	4.56	4.5	4	5	4.5	4.44	3.76	3.5	3.65	1.95	1.47
12	資質	能力	3.85	3.47	3.5	3.5	4	4	3.88	4.25	4.06	4.19	1.53	1.63
13	預算	計劃	3.95	4.16	3.5	4	4	4	4.31	4.06	4.5	4.12	2.42	1.89
14	緣分	友情	4.2	3.94	3.5	4	4	4	4	4.27	4.44	4.67	1.38	1.86
15	星座	生肖	3.9	3.9	4	4	4	4	4.44	4.07	4.75	4.67	2.48	2.48
16	詩歌	樂曲	4.2	4.14	4.5	4	4	4.5	4.13	4	4.31	4	2.84	2.95
17	友誼	親情	4	3.65	4	4	4	4	4.63	4	4.63	4.12	1.74	1.74
18	約定	信用	4.45	3.56	3.5	3.5	4.5	4	4.13	4.13	4.13	4.38	1.84	1.74
19	供應	需求	4.5	3.94	4	4	5	5	4.13	4.38	4.19	4.25	2.42	1.84
20	數量	成本	3.55	3.27	2	2.5	4	3.5	4.69	4.38	4.31	4.31	2.42	2.05
21	意見	勸告	3.7	3.31	4	3.5	4	4	4.56	4.06	3.94	3.94	2.05	1.79
22	界限	邊緣	3.15	3.37	4	4	3.5	3.5	3.69	4.19	4.31	4.13	1.74	2.26
23	定義	公式	3.95	3.53	3	3	4	3.5	4.13	4	4.31	3.93	1.62	2.52
24	興趣	志向	4.2	3.74	4	4	4.5	4	4.88	4.24	3.75	3.82	2.11	1.53
25	型號	版本	4.05	3.88	4.5	3.5	4	4	4.44	4.27	4.13	3.93	3.19	2.19
26	姓名	年齡	3.9	4.11	3	3	4	3.5	4.81	4.8	4.88	4.87	2.9	2.86
27	鄰里	社區	3.95	3.96	3	4	4	4	4.13	4.18	4.25	4	2.21	2.37
28	激情	浪漫	4	3.79	4	3.5	4	4	3.81	3.88	3.81	3.88	1.58	1.32
29	利潤	增幅	3.95	3.64	3	3	4	4	4.13	4.44	4.38	4.25	2.21	2.37
30	範圍	領域	3.5	3.69	4	4	4	4	4.25	4.25	3.81	4	2.21	1.95

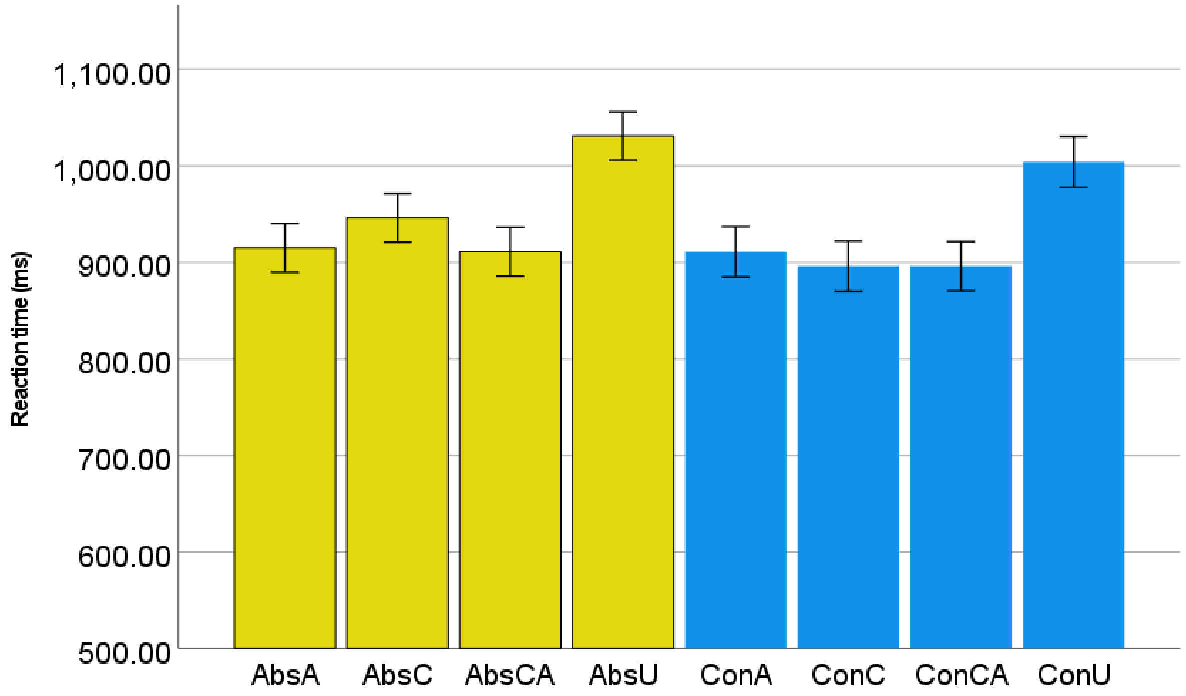
Semantic priming: stimulus design

	Purely categorical (C)	Purely associative (A)	Both categorical & associative (CA)	Unrelated
Concrete	輪船 – 火車 ferry – train	白髮 – 老人 white hair – elder	火箭 – 衛星 rocket – satellite	花朵 – 雪糕 flower – ice-cream
Abstract	心腸 – 品性 heart – character	保險 – 賠償 insurance - compensation	方法 – 步驟 method – step	夢想 – 判決 dream – verdict

- **Stimulus design**
  - 36 pairs per condition
  - SOA = 800 ms (due to auditory mode of presentation, SOA much longer than typical visual studies)
  - Phonological overlap were avoided as much as possible (no sharing of base syllable)

Behavioral results (Accuracy)





Priming effect = Unrelated – other conditions (A/C/CA)

Correlates of semantic priming effect

Pearson's correlation

Correlations

		AverageSP	AbsSP	ConSP	Age	Education	MoCA	Synonym	Shipley	StroopCW	DigitSpan	HKLLT	TOH
AverageSP	Pearson Correlation	1	.796**	.788**	.502**	-.042	-.063	.201*	.083	-.325**	-.245*	-.197*	-.337**
	Sig. (2-tailed)		<.001	<.001	<.001	.673	.529	.041	.406	<.001	.013	.046	<.001
	N	103	103	103	103	103	103	103	103	103	103	103	103

hyper-priming effect

Partial correlation

Correlations

Control Variables			AverageSP	Age
Synonym & Education & MoCA & Shipley & StroopCW & DigitSpan & HKLLT & TOH	AverageSP	Correlation	1.000	.309
		Significance (2-tailed)	.	.002
		df	0	93
	Age	Correlation	.309	1.000
		Significance (2-tailed)	.002	.
		df	93	0

Linear regression

Model		Unstandardized Coefficients B	Unstandardized Coefficients Std. Error	Standardized Coefficients Beta	t	Sig.
1	(Constant)	64.296	59.561		1.079	.283
	Age	1.076	.339	.424	3.171	.002
	Education	-1.335	1.420	-.091	-.941	.349
	Synonym	1.309	1.510	.086	.867	.388
	Shipley	.619	.627	.101	.987	.326
	StroopCW	-.167	.470	-.040	-.356	.723
	DigitSpan	-4.259	2.831	-.139	-1.504	.136
	HKLLT	-.156	1.596	-.010	-.098	.922
	TOH	-.080	1.178	-.008	-.068	.946

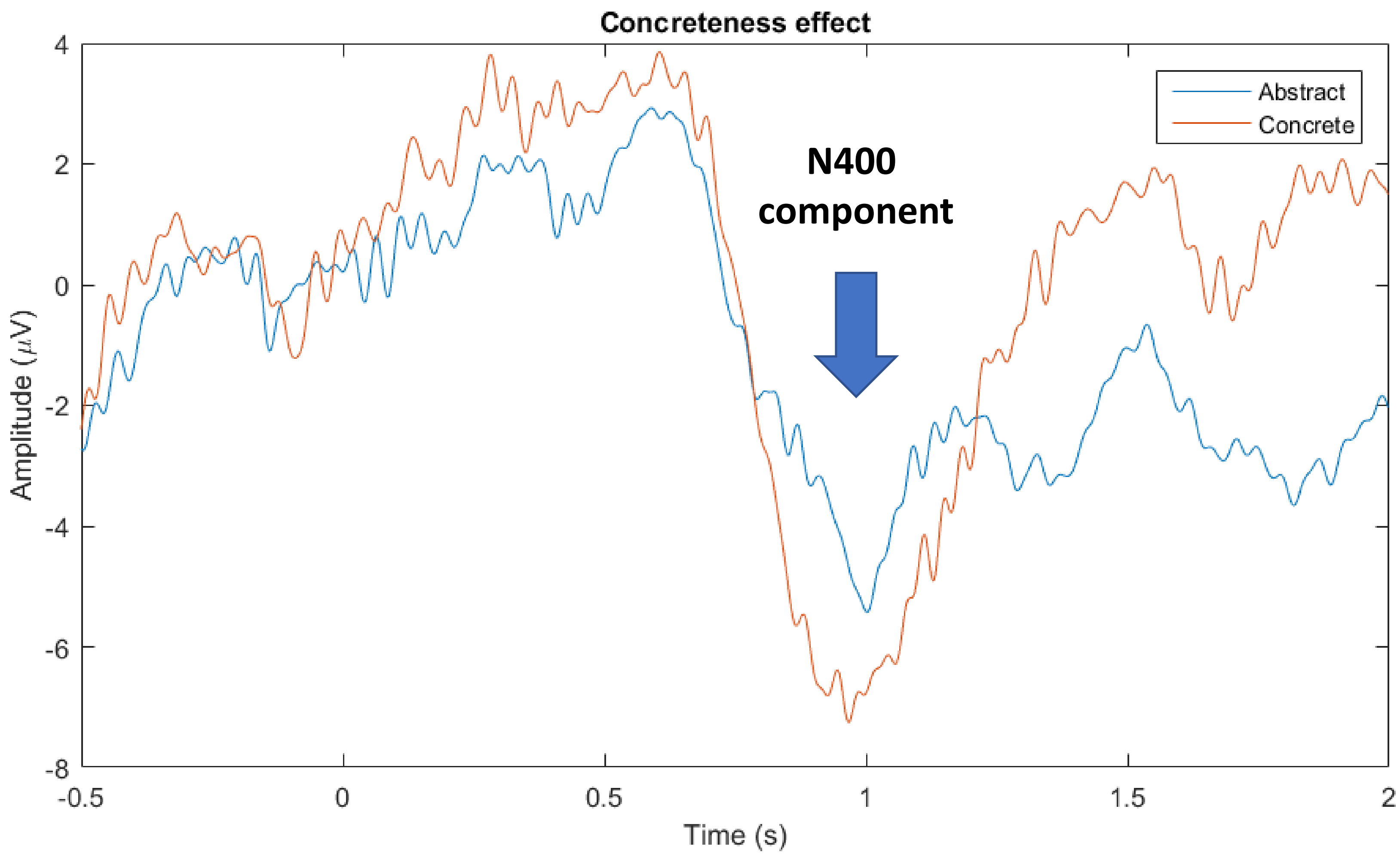
a. Dependent Variable: AverageSP

Interpretations

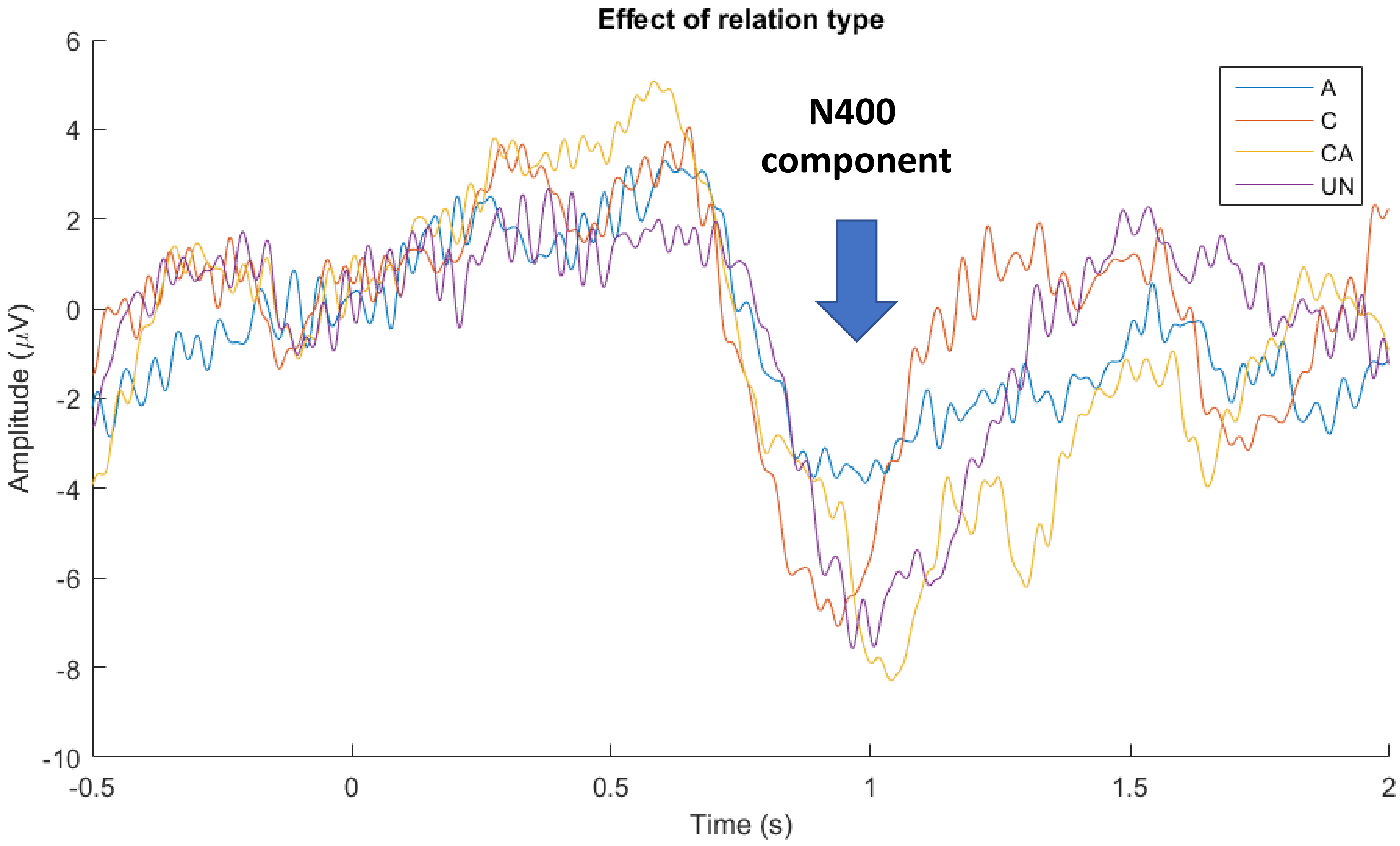
- The analyses thus far suggested that the **hyper-priming effect (i.e., the age-related increase in semantic priming effect)** is a genuine effect that could not be accounted for by non-semantic cognitive domains, nor could it be accounted for by demographical factors (e.g., education).

- It is plausible that accurate behavioral measures of semantic functions or other **more fundamental factors (neural?)** are necessary to account for the hyper-priming effect.

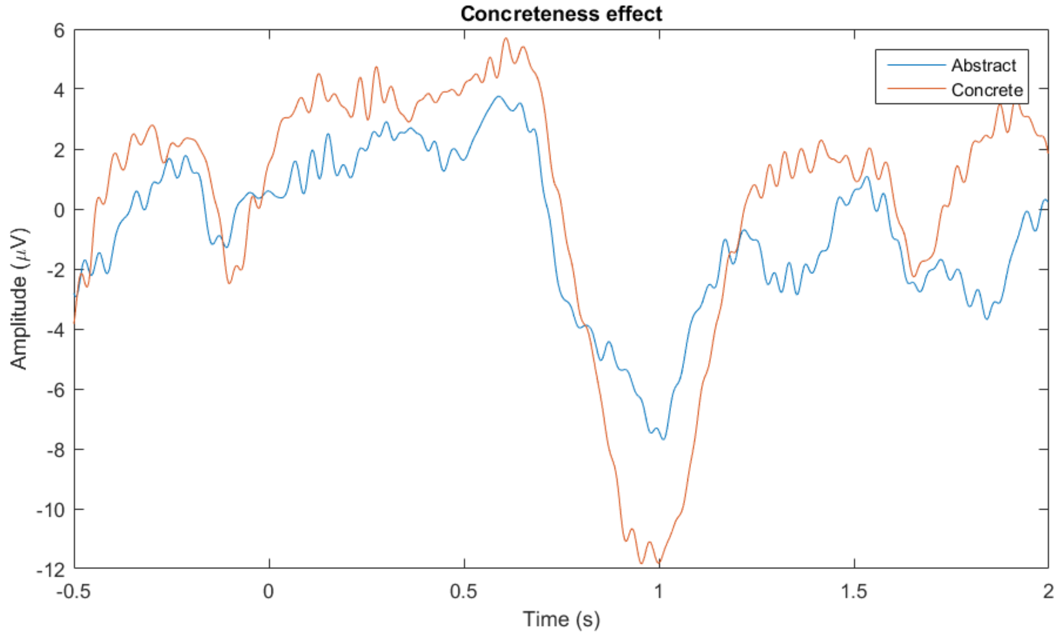
Effect of concreteness



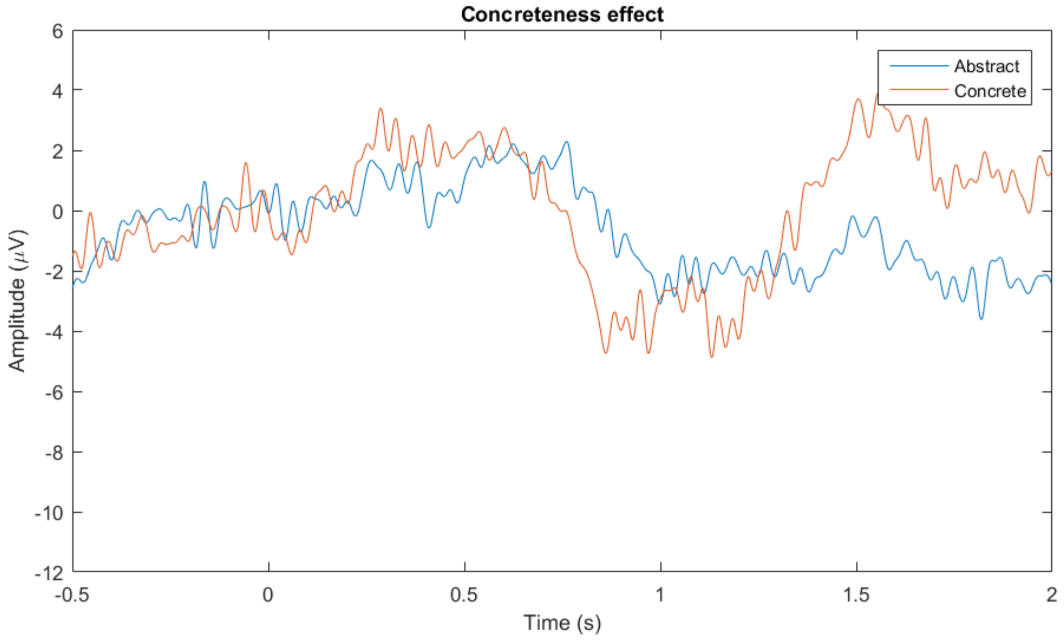
Effect of relation type



Effect of age



Older adults (11 participants)



Younger adults (21 participants)

MRI session (task sequence)

Name	Purpose	Basis of the parameter choice	Minutes (approximate)
Localizer	Setting field of view		Several seconds
T1 MPRAGE	Structural MRI	ADNI	5 minutes
Field map (AP) Field map (PA)	Correcting distortion	HCP	8 seconds 8 seconds
Functional localizer (Run 1) ***Functional localizer (Run 2)*** ***Semantic priming (Run 1)*** ***Semantic priming (Run 2)***	Critical tasks	HCP; multiband sequence with good temporal resolution (TR = 800 ms)	8 minutes 8 minutes 11 minutes 11 minutes
Field map (AP) Field map (PA)	Correcting distortion	HCP	8 seconds 8 seconds

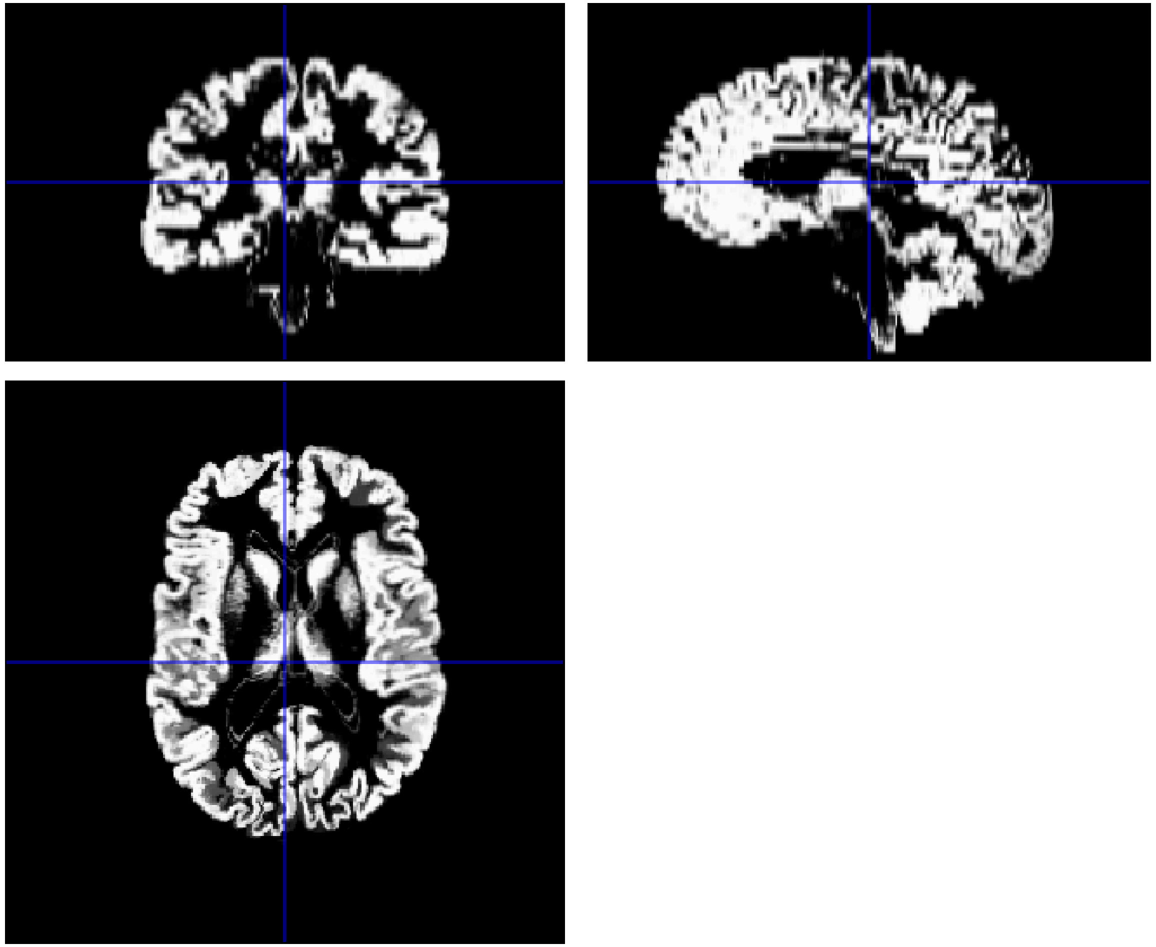
Post test: ***incidental verbal recognition memory test (old / new judgment)***

Post-test: implicit verbal recognition memory

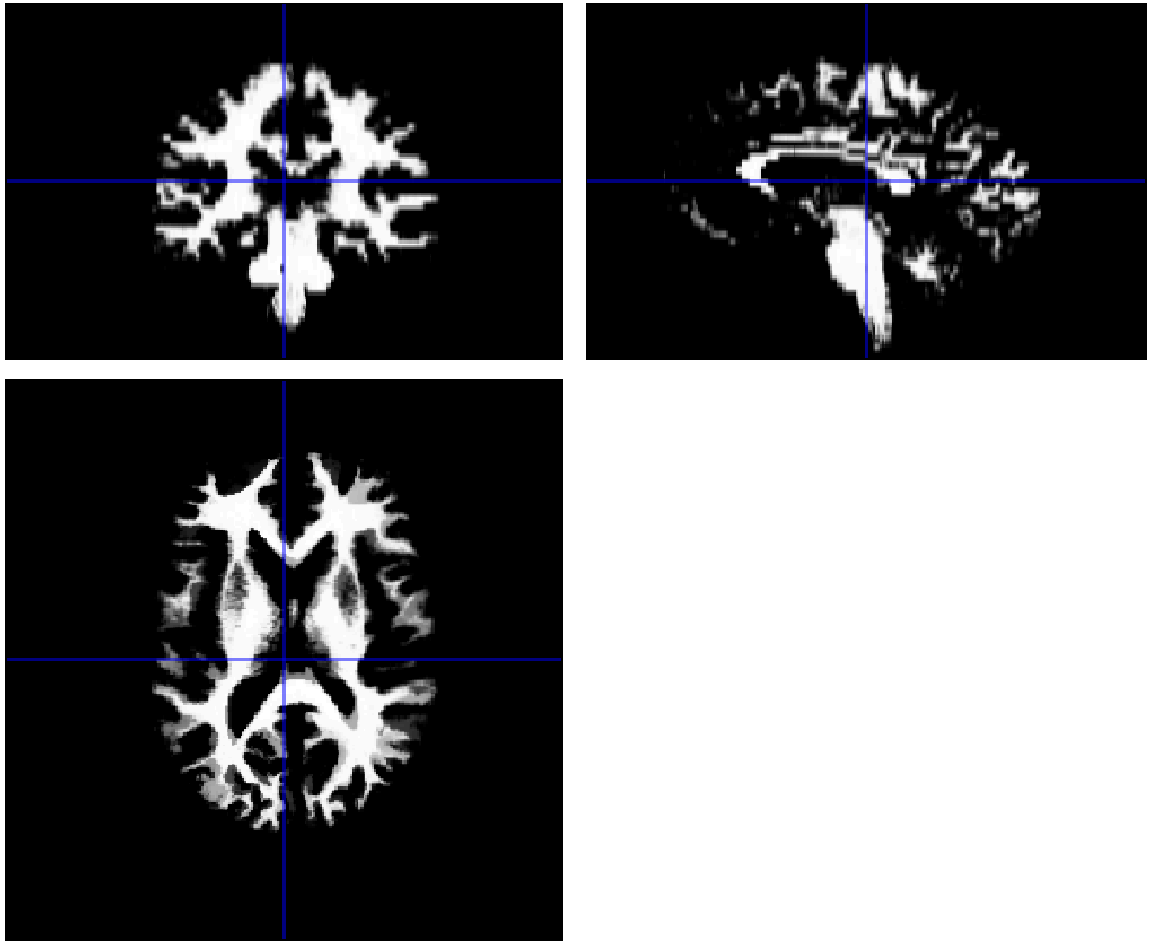
- **Task**: Old / new judgment
- **Old stimuli**
  - 6 primes each from eight conditions [Concreteness x Relation]
  - 6 targets each from eight conditions [Concreteness x Relation]
- **New stimuli**
  - **48 concrete** and **48 abstract** stimuli that are matched with **old words** in psycholinguistic properties (familiarity / concreteness / AoA / stroke count)
- **Predictions**: Participants with larger semantic priming effect will exhibit
  - Better recognition memory overall;
  - Better recognition memory for concrete than abstract targets;
  - Better recognition memory for related pairs (CA/C/A) than unrelated pairs (U);
  - Better recognition memory for targets than primes.

Segmentation (grey and white matter)

Grey matter

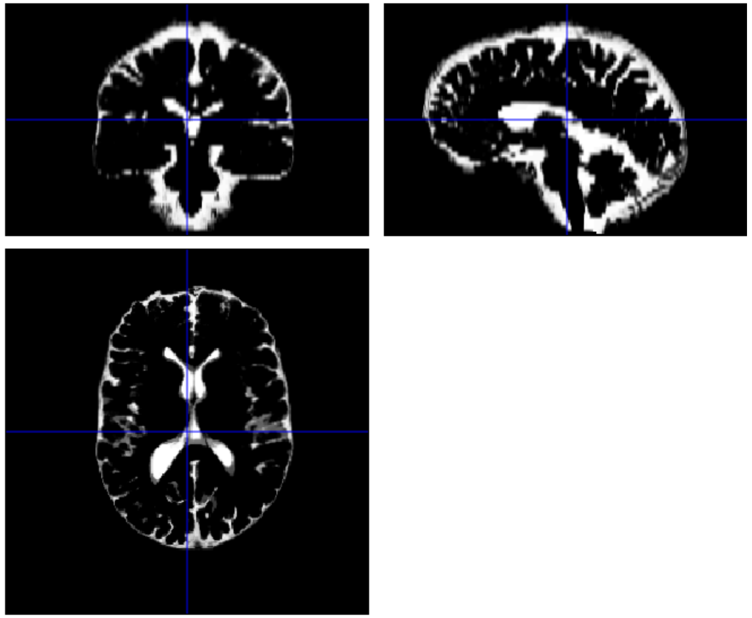


White matter

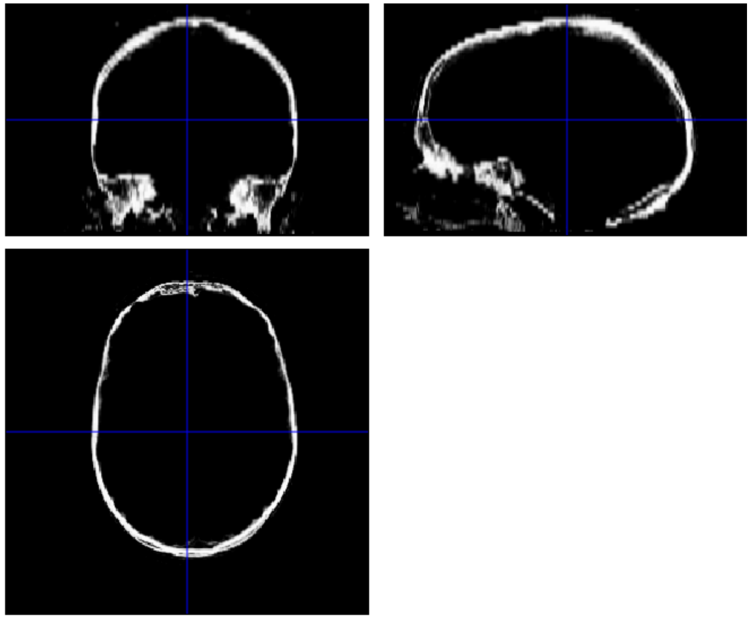


Segmentation (cerebrospinal fluid, meninges, and skull)

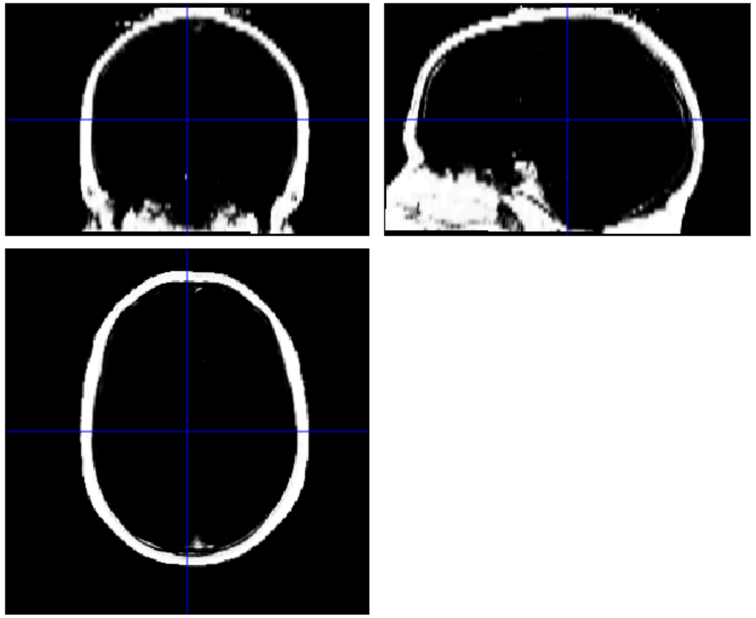
Cerebrospinal fluid



Meninges



Skull



From Walhovd, K. B., Westlye, L. T., Amlien, I., Espeseth, T., Reinvang, I., Raz, N., ... & Fjell, A. M. (2011). Consistent neuroanatomical age-related volume differences across multiple samples. *Neurobiology of Aging*, *32*(5), 916-932.

Table 3
Mean volume of the different neuroanatomical structures per decade.

	Total sample (*N* = 883)													
	18–29 years (*N* = 262)		30–39 years (*N* = 109)		40–49 years (*N* = 159)		50–59 years (*N* = 100)		60–69 years (*N* = 110)		70–79 years (*N* = 105)		80–95 years (*N* = 38)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cerebral Cor	517426	66685	489079	69076	484994	73159	446856	60459	419190	68791	393507	58007	389445	39685
Cerebral WM	448369	55455	465638	59881	473373	70145	451591	57500	427932	59294	393931	53765	360263	53355
Lat Vent	12659	6902	15046	9093	16152	9943	17472	9330	24566	12949	34205	17344	41336	17985
Inf Lat Vent	651	363	724	434	705	432	712	401	1045	671	1742	1130	2499	1191
Cerebel WM	28320	3506	28543	3444	28410	3747	27360	3587	25787	3544	24452	3198	22862	4006
Cerebel Cor	109909	13173	108925	12313	107773	13778	101211	13572	97125	13010	90332	13464	90595	9440
Thalamus	14002	1518	14037	1431	13624	1600	12749	1449	12241	1513	11510	1358	10931	1182
Caudate	7848	981	7319	887	7139	901	6939	850	6853	1011	6975	972	7285	1269
Putamen	12507	1400	11312	1360	10707	1136	10206	1127	9640	1034	9520	1158	9035	1209
Pallidum	3638	452	3395	481	3236	394	3051	435	2981	485	2889	336	2646	466
Hippocampus	8214	889	8319	941	8368	1044	8101	1027	7467	1106	6865	979	6201	730
Amygdala	3540	459	3442	467	3400	495	3216	477	3025	524	2766	440	2679	507
Accumbens	1492	266	1263	244	1175	199	1142	229	1060	178	1013	181	1038	180
3rd Vent	1032	286	992	361	1033	356	1173	406	1419	526	1813	574	1927	708
4th Vent	1979	576	1945	640	1801	514	1847	491	2016	666	2126	664	2077	665
Brainstem	21456	2385	22186	2413	22206	2696	21444	2594	21277	2732	20179	2565	19086	2455
CSF	1195	241	1241	338	1273	269	1245	281	1412	330	1542	654	1606	496
Total volume	1176723	125178	1163458	130877	1164404	151413	1093865	126705	1034578	135408	963939	120410	922066	98074
ICV	1586302	161092	1615561	173216	1610050	185966	1552345	157821	1534473	159132	1538938	175808	1488398	171561

Females ($N = 528$)

	18–29 years ($N = 154$)		30–39 years ($N = 58$)		40–49 years ($N = 83$)		50–59 years ($N = 64$)		60–69 years ($N = 72$)		70–79 years ($N = 67$)		80–95 years ($N = 30$)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cerebral Cor	490631	57077	460475	53466	453442	57940	425692	52015	398916	59567	378820	49812	389744	38415
Cerebral WM	427040	46766	439966	43353	439631	52271	424193	40860	406040	47102	378277	50723	357302	46707
Lat Vent	11262	4941	13202	6490	15018	10420	14436	6368	23399	12715	30458	16178	38390	16059
Inf Lat Vent	639	307	651	364	682	472	625	379	972	667	1578	1066	2154	967
Cerebel WM	27375	2757	27404	3238	27310	3104	26208	3219	25006	2956	24148	3370	22853	3588
Cerebel Cor	104270	9742	103237	9566	101066	10112	95664	10922	93178	11080	87705	12021	89267	7308
Thalamus	13367	1257	13468	1140	13018	1411	12282	1224	11643	1136	11190	1388	10805	822
Caudate	7576	883	7072	709	6931	851	6649	630	6597	904	6830	863	7288	1072
Putamen	12060	1278	10832	1261	10385	1033	9882	1003	9382	903	9093	759	9134	1148
Pallidum	3477	418	3216	452	3075	381	2916	304	2857	496	2807	298	2624	398
Hippocampus	7889	737	8075	904	7954	870	7896	994	7182	837	6726	890	6166	688
Amygdala	3396	439	3241	365	3169	395	3039	379	2862	445	2655	358	2598	357
Accumbens	1461	246	1202	237	1154	206	1108	215	1030	186	1005	180	1035	154
3rd Vent	978	231	912	293	978	343	1061	300	1327	485	1646	534	1708	482
4th Vent	1889	499	1834	567	1706	500	1819	475	1959	710	2051	687	2033	704
Brainstem	20518	2021	21265	2092	21205	2238	20505	2165	20353	2201	19394	2095	18910	2166
CSF	1136	226	1184	351	1186	255	1132	201	1365	334	1451	761	1480	369
Total volume	1119061	102916	1099454	87918	1088340	107907	1036033	96939	985044	108815	928650	104816	917726	85065
ICV	1510744	125832	1533802	131432	1531369	157510	1471598	101797	1465030	124339	1468898	140686	1451682	130944

Males ($N = 355$)

	18–29 years ($N = 108$)		30–39 years ($N = 51$)		40–49 years ($N = 76$)		50–59 years ($N = 36$)		60–69 years ($N = 38$)		70–79 years ($N = 38$)		80–95 years ($N = 8$)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cerebral Cor	555635	60678	521609	70846	519452	72801	484482	56517	457605	69402	419400	62870	388322	47000
Cerebral WM	478784	52778	494832	62998	510222	68864	500298	50339	469412	58311	421531	48060	371369	76358
Lat Vent	14650	8630	17144	11052	17389	9305	22870	11242	26776	13270	40812	17563	52386	21551
Inf Lat Vent	670	431	807	493	729	386	868	396	1184	666	2031	1196	3791	1097
Cerebel WM	29669	3999	29838	3233	29612	4030	29409	3316	27268	4098	24988	2833	22897	5611
Cerebel Cor	117948	13288	115394	11957	115097	13564	111071	12250	104604	13240	94963	14741	95572	14625
Thalamus	14909	1397	14684	1462	14285	1538	13580	1460	13374	1503	12074	1111	11403	2064
Caudate	8235	989	7599	988	7366	904	7455	950	7338	1036	7231	1105	7272	1938
Putamen	13145	1324	11858	1270	11059	1145	10781	1118	10129	1100	10273	1351	8664	1439
Pallidum	3868	396	3599	433	3411	330	3291	526	3216	365	3034	355	2727	693
Hippocampus	8677	884	8597	913	8821	1035	8466	996	8006	1343	7111	1089	6331	908
Amygdala	3744	407	3672	468	3652	471	3530	476	3336	526	2962	503	2985	835
Accumbens	1536	288	1333	235	1197	191	1202	244	1118	146	1027	184	1050	269
3rd Vent	1108	337	1083	409	1092	362	1372	492	1593	562	2107	527	2749	843
4th Vent	2108	651	2070	698	1904	512	1895	523	2124	569	2257	608	2244	493
Brainstem	22794	2229	23233	2343	23299	2741	23113	2473	23029	2808	21564	2752	19747	3433
CSF	1279	239	1307	312	1367	252	1445	295	1503	305	1703	356	2079	643
Total volume	1258945	107088	1236248	134276	1247473	148899	1196677	107274	1128433	132181	1026159	122167	938339	143108
ICV	1694042	143966	1708541	168946	1695978	177193	1695896	136681	1666049	133301	1662430	164399	1626083	238950

% change per decade
From Walhovd et al. (2011)

Percentage change per decade for the total sample based on raw volumes.

	18–29 to 30–39	30–39 to 40–49	40–49 to 50–59	50–59 to 60–69	60–69 to 70–79	70–79 to 80–95	18–29 to 80–95
Cerebral Cor	−5.5	−.8	−7.9	−6.2	−6.1	−1.0	−24.7
Cerebral WM	3.9	1.7	−4.6	−5.2	−7.9	−8.5	−19.7
Lat Vent	18.9	7.4	8.2	40.6	39.2	20.8	226.5
Inf Lat Vent	11.2	−2.6	1.0	46.8	66.7	43.5	283.9
Cerebel WM	.8	−.5	−3.7	−5.7	−5.2	−6.5	−19.3
Cerebel Cor	−.9	−1.1	−6.1	−4.0	−7.0	.3	−17.6
Thalamus	.2	−2.9	−6.4	−4.0	−6.0	−5.0	−21.9
Caudate	−6.7	−2.5	−2.8	−1.2	1.8	4.4	−7.2
Putamen	−9.6	−5.3	−4.7	−5.5	−1.2	−5.1	−27.8
Pallidum	−6.7	−4.7	−5.7	−2.3	−3.1	−8.4	−27.3
Hippocampus	1.3	.6	−3.2	−7.8	−8.1	−9.7	−24.5
Amygdala	−2.8	−1.2	−5.4	−5.9	−8.6	−3.1	−24.3
Accumbens	−15.3	−7.0	−2.8	−7.2	−4.4	2.5	−30.4
3rd Vent	−3.9	4.1	13.6	21.0	27.8	6.3	86.7
4th Vent	−1.7	−7.4	2.6	9.1	5.5	−2.3	5.0
Brainstem	3.4	.1	−3.4	−.8	−5.2	−5.4	−11.0
CSF	3.8	2.6	−2.2	13.4	9.2	4.2	34.4
Total volume	−1.1	.1	−6.1	−5.4	−6.8	−4.3	−21.6

Cor: cortex; WM: white matter; Lat: lateral; Inf: inferior; Vent: ventricles; CSF: cerebrospinal fluid; Total volume: the sum of all the other structures (CSF and ventricles not included).

CROSS-SECTIONAL DIFFERENCES IN BRAIN VOLUMES (in mm^3)

	All							Male							Female						
	18-29	30-39	40-49	50-59	60-69	70-79	80-89	18-29	30-39	40-49	50-59	60-69	70-79	80-89	18-29	30-39	40-49	50-59	60-69	70-79	80-89
Left-Lateral-Ventricle	6804.9	7099.9	9196.7	10853.6	13087.0	14910.5	26324.9	7439.6	8038.0	10158.3	12033.5	13526.6	17227.9	41526.1	6233.6	6005.5	8662.5	9526.3	12687.5	12013.7	11123.6
Left-Inf-Lat-Vent	346.8	301.4	293.3	390.9	422.6	544.1	451.3	321.1	343.7	345.6	381.0	491.2	697.0	501.5	369.9	252.2	264.2	402.1	360.3	352.9	401.0
Left-Hippocampus	4276.7211	4037.4385	3970.4857	3941.2588	3892.819	3708.9556	3145.3	4535.7889	4136.3286	3991.84	4073.7667	4098.65	3757.55	3277.3	4043.56	3922.0667	3958.6222	3792.1875	3705.7	3648.2125	3013.3
Left-Amygdala	1655.7789	1570.7077	1547.9	1559.2412	1510.8857	1421.7167	1110.65	1805.4222	1557.2	1553.58	1612.0111	1575.59	1470.34	1153.4	1521.1	1586.4667	1544.7444	1499.875	1452.0636	1360.9375	1067.9
Left-Thalamus	8969.9263	8018.8538	7839.4929	7634.9412	7283.1333	6868.9444	7029.35	9433.5	8101.7286	8273.62	8136.0667	7532.34	7057.26	8061.4	8552.71	7922.1667	7598.3111	7071.175	7056.5818	6633.55	5997.3
Left-Caudate	3912.2421	3579.4385	3385.6643	3215.0353	3232.1238	3314.9611	3332.25	4051.2444	3722.3286	3677.3	3137.2222	3246.12	3380.82	3295.4	3787.14	3412.7333	3223.6444	3302.575	3219.4	3232.6375	3369.1
Left-Putamen	5327.2632	5196.4538	4744.1857	4793.2588	4588.3619	4359.0389	4054.55	5578.5	5318.1143	4903.38	5069.8667	4838.26	4377.58	4287.1	5101.15	5054.5167	4655.7444	4482.075	4361.1818	4335.8625	3822
Left-Pallidum	2195.2368	2080.9692	2065.9357	2006.5235	2041.1905	1945.1167	1912.75	2323.8111	2142.1857	2086.52	2107.9222	2190.44	1956.57	2107	2079.52	2009.55	2054.5	1892.45	1905.5091	1930.8	1718.5
Left-Accumbens-area	495.48947	461.46923	380.95	398.94118	383.31905	342.36667	249.75	574.76667	458.97143	378.08	410.68889	385.04	359.37	273.8	424.14	464.38333	382.54444	385.725	381.75455	321.1125	225.7
Left-Cerebellum-White-Matter	15992.537	15747.292	14679.414	14474.041	14209.967	13494.528	12105.9	17018.144	15949.7	15188.64	14813.4	14801.28	13812.47	13775	15069.49	15511.15	14396.511	14092.263	13672.409	13097.1	10436.8
Left-Cerebellum-Cortex	56868.3	54129.108	50868.029	50545.524	49829.514	48512.894	44239.8	62172.078	55523.5	54585.48	52384	52076.8	48725.39	50733.7	52094.9	52502.317	48802.778	48477.238	47786.527	48247.275	37745.9
Right-Lateral-Ventricle	5896.8	5508.6	8589.1	8898.4	11895.9	12881.4	22356.5	6543.4	6227.8	8875.4	9627.6	11291.0	14846.0	34340.0	5314.8	4669.5	8430.0	8078.1	12445.8	10425.6	10373.0
Right-Inf-Lat-Vent	362.2	327.7	346.4	346.1	424.8	545.3	523.7	357.5	373.7	398.1	367.0	450.8	677.0	819.9	366.4	274.1	317.6	322.7	401.1	380.6	227.4
Right-Hippocampus	4454.7	4268.5	4131.7	4179.9	4064.8	3843.1	3226.7	4545.3	4330.4	4290.6	4336.2	4294.4	3845.5	3340.0	4373.2	4196.2	4043.4	4004.0	3856.2	3840.1	3113.3
Right-Amygdala	1768.6	1702.6	1651.0	1647.7	1684.8	1580.4	1391.9	1919.1	1777.7	1716.4	1707.9	1826.4	1640.5	1340.2	1633.1	1615.0	1614.6	1580.0	1556.1	1505.4	1443.6
Right-Thalamus	8606.3	7990.0	7445.6	7414.1	7072.3	6736.4	6713.4	9089.6	8211.6	7779.1	7782.9	7500.8	6838.0	7225.8	8171.4	7731.4	7260.3	6999.1	6682.8	6609.4	6200.9
Right-Caudate	4010.7	3630.3	3490.5	3339.9	3345.4	3385.4	3600.4	4150.0	3762.9	3877.6	3301.5	3352.8	3413.3	3876.7	3885.4	3475.7	3275.4	3383.1	3338.6	3350.6	3324.0
Right-Putamen	5576.2	5295.4	4923.1	4895.1	4616.0	4415.0	3996.8	5785.8	5377.8	5215.9	5163.9	4830.0	4416.9	3988.0	5387.5	5199.3	4760.4	4592.7	4421.4	4412.6	4005.5
Right-Pallidum	2146.2	1995.3	2054.9	2006.1	2028.3	1890.5	1726.3	2259.6	2026.3	2123.0	2103.8	2112.6	1855.9	1864.4	2044.2	1959.3	2017.0	1896.3	1951.7	1933.7	1588.1
Right-Accumbens-area	602.1	561.7	471.5	493.9	476.1	413.9	393.9	663.5	561.2	472.4	528.9	496.2	394.4	454.6	546.8	562.2	471.0	454.5	457.9	438.3	333.1
Right-Cerebellum-White-Matter	15296.4	15004.5	14293.7	13764.9	13890.8	12635.1	12229.0	16534.6	15221.3	15424.8	14413.3	14471.4	13122.5	14389.8	14182.0	14751.6	13665.4	13035.5	13363.0	12025.9	10068.2
Right-Cerebellum-Cortex	56846.2	54542.2	51375.7	50827.9	49863.5	49437.5	45250.6	61817.2	56286.0	54838.0	52662.8	52199.6	49799.9	51732.9	52372.3	52507.8	49452.2	48763.5	47739.7	48984.4	38768.3
CerebralWhiteMatterVol	22549.2	21139.7	20885.0	21021.9	21268.3	20460.0	19079.0	24217.1	21486.8	22025.8	21972.1	22346.5	20848.9	22619.5	21048.1	20734.8	20251.2	19953.1	20288.2	19973.9	15538.5
Brain-Stem	488197.5	435672.6	455970.5	443449.2	443470.2	413178.3	362579.0	526021.7	448572.4	487294.6	473411.9	469872.7	427853.1	437161.0	454155.8	420622.8	438568.2	409741.1	419467.9	394834.8	287997.0
SubCortGrayVol	64077.1	59403.0	57078.6	56625.5	55227.0	52914.0	50154.0	67708.9	60627.6	59663.8	58950.6	57744.7	53842.0	54057.0	60808.5	57974.3	55642.4	54009.8	52938.2	51754.0	46251.0
TotalGrayVol	716195.9	650541.0	639270.3	622720.6	608501.2	596719.8	570208.3	770845.4	665746.3	681871.9	645399.7	637360.3	614363.2	634380.9	667011.3	632801.4	615602.7	597206.6	582265.7	574665.4	506035.7
EstimatedTotalIntraCranialVol	1583643.2	1470497.1	1507530.3	1494315.5	1507022.2	1487217.1	1489408.6	1661868.0	1511746.6	1573365.6	1575781.5	1599993.3	1544619.3	1758387.9	1513240.9	1422372.7	1470955.2	1402666.2	1422503.0	1415464.4	1520429.3

CROSS-SECTIONAL DIFFERENCES IN BRAIN VOLUME CHANGES

% change per annum	All						Male						Female					
	30-39	40-49	50-59	60-69	70-79	80-89	30-39	40-49	50-59	60-69	70-79	80-89	30-39	40-49	50-59	60-69	70-79	80-89
Left-Lateral-Ventricle	0.4	3.0	1.8	2.1	1.4	7.7	0.8	2.6	1.8	1.2	2.7	14.1	-0.4	4.4	1.0	3.3	-0.5	-0.7
Left-Inf-Lat-Vent	-1.3	-0.3	3.3	0.8	2.9	-1.7	0.7	0.1	1.0	2.9	4.2	-2.8	-3.2	0.5	5.2	-1.0	-0.2	1.4
Left-Hippocampus	-0.6	-0.2	-0.1	-0.1	-0.5	-1.5	-0.9	-0.3	0.2	0.1	-0.8	-1.3	-0.3	0.1	-0.4	-0.2	-0.2	-1.7
Left-Amygdala	-0.5	-0.1	0.1	-0.3	-0.6	-2.2	-1.4	0.0	0.4	-0.2	-0.7	-2.2	0.4	-0.3	-0.3	-0.3	-0.6	-2.2
Left-Thalamus	-1.1	-0.2	-0.3	-0.5	-0.6	0.2	-1.4	0.2	-0.2	-0.7	-0.6	1.4	-0.7	-0.4	-0.7	0.0	-0.6	-1.0
Left-Caudate	-0.9	-0.5	-0.5	0.1	0.3	0.1	-0.8	-0.1	-1.5	0.3	0.4	-0.3	-1.0	-0.6	0.2	-0.3	0.0	0.4
Left-Putamen	-0.2	-0.9	0.1	-0.4	-0.5	-0.7	-0.5	-0.8	0.3	-0.5	-1.0	-0.2	-0.1	-0.8	-0.4	-0.3	-0.1	-1.2
Left-Pallidum	-0.5	-0.1	-0.3	0.2	-0.5	-0.2	-0.8	-0.3	0.1	0.4	-1.1	0.8	-0.3	0.2	-0.8	0.1	0.1	-1.1
Left-Accumbens-area	-0.7	-1.7	0.5	-0.4	-1.1	-2.7	-2.0	-1.8	0.9	-0.6	-0.7	-2.4	0.9	-1.8	0.1	-0.1	-1.6	-3.0
Left-Cerebellum-White-Matter	-0.2	-0.7	-0.1	-0.2	-0.5	-1.0	-0.6	-0.5	-0.2	0.0	-0.7	0.0	0.3	-0.7	-0.2	-0.3	-0.4	-2.0
Left-Cerebellum-Cortex	-0.5	-0.6	-0.1	-0.1	-0.3	-0.9	-1.1	-0.2	-0.4	-0.1	-0.6	0.4	0.1	-0.7	-0.1	-0.1	0.1	-2.2
Right-Lateral-Ventricle	-0.7	5.6	0.4	3.4	0.8	7.4	-0.5	4.3	0.8	1.7	3.1	13.1	-1.2	8.1	-0.4	5.4	-1.6	-0.1
Right-Inf-Lat-Vent	-1.0	0.6	0.0	2.3	2.8	-0.4	0.5	0.7	-0.8	2.3	5.0	2.1	-2.5	1.6	0.2	2.4	-0.5	-4.0
Right-Hippocampus	-0.4	-0.3	0.1	-0.3	-0.5	-1.6	-0.5	-0.1	0.1	-0.1	-1.0	-1.3	-0.4	-0.4	-0.1	-0.4	0.0	-1.9
Right-Amygdala	-0.4	-0.3	0.0	0.2	-0.6	-1.2	-0.7	-0.3	0.0	0.7	-1.0	-1.8	-0.1	0.0	-0.2	-0.2	-0.3	-0.4
Right-Thalamus	-0.7	-0.7	0.0	-0.5	-0.5	0.0	-1.0	-0.5	0.0	-0.4	-0.9	0.6	-0.5	-0.6	-0.4	-0.5	-0.1	-0.6
Right-Caudate	-0.9	-0.4	-0.4	0.0	0.1	0.6	-0.9	0.3	-1.5	0.2	0.2	1.4	-1.1	-0.6	0.3	-0.1	0.0	-0.1
Right-Putamen	-0.5	-0.7	-0.1	-0.6	-0.4	-0.9	-0.7	-0.3	-0.1	-0.6	-0.9	-1.0	-0.3	-0.8	-0.4	-0.4	0.0	-0.9
Right-Pallidum	-0.7	0.3	-0.2	0.1	-0.7	-0.9	-1.0	0.5	-0.1	0.0	-1.2	0.0	-0.4	0.3	-0.6	0.3	-0.1	-1.8
Right-Accumbens-area	-0.7	-1.6	0.5	-0.4	-1.3	-0.5	-1.5	-1.6	1.2	-0.6	-2.1	1.5	0.3	-1.6	-0.4	0.1	-0.4	-2.4
Right-Cerebellum-White-Matter	-0.2	-0.5	-0.4	0.1	-0.9	-0.3	-0.8	0.1	-0.7	0.0	-0.9	1.0	0.4	-0.7	-0.5	0.3	-1.0	-1.6
Right-Cerebellum-Cortex	-0.4	-0.6	-0.1	-0.2	-0.1	-0.8	-0.9	-0.3	-0.4	-0.1	-0.5	0.4	0.0	-0.6	-0.1	-0.2	0.3	-2.1
CerebralWhiteMatterVol	-0.6	-0.1	0.1	0.1	-0.4	-0.7	-1.1	0.3	0.0	0.2	-0.7	0.8	-0.1	-0.2	-0.1	0.2	-0.2	-2.2
Brain-Stem	-1.1	0.5	-0.3	0.0	-0.7	-1.2	-1.5	0.9	-0.3	-0.1	-0.9	0.2	-0.7	0.4	-0.7	0.2	-0.6	-2.7
SubCortGrayVol	-0.7	-0.4	-0.1	-0.2	-0.4	-0.5	-1.0	-0.2	-0.1	-0.2	-0.7	0.0	-0.5	-0.4	-0.3	-0.2	-0.2	-1.1
TotalGrayVol	-0.9	-0.2	-0.3	-0.2	-0.2	-0.4	-1.4	0.2	-0.5	-0.1	-0.4	0.3	-0.5	-0.3	-0.3	-0.3	-0.1	-1.2
EstimatedTotalIntraCranialVol	-0.7	0.3	-0.1	0.1	-0.1	0.0	-0.9	0.4	0.0	0.2	-0.3	1.4	-0.6	0.3	-0.5	0.1	0.0	-1.4

Take home messages

- The consequences of the structural and functional brain changes on crystallized intelligence, particularly semantic processing, have not yet been fully determined.

- Thus far, we have found a genuine hyper priming effect (an age-related increase in auditory semantic priming effect) that could not be accounted for merely by cognitive performance.

- Other measures of semantic processing and brain measures may shed light on the nature of the effect.

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