TITLE

Brain activation for language and its relationship to cognitive and linguistic measures

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ABSTRACT

Language learning and use are complex cognitive skills requiring domain-general cognition and sensori-motor skills, these also being important for numerical and music processing. Previous studies have explored behavioural associations across domains and neural underpinnings of specific abilities, yet less work has examined these questions together in the same participants. We collected data from 152 participants on behavioural measures of language, reading, multilingual experience, cognition, musicality, arithmetic, and motor skills, along with fMRI data during L1 story listening. Participants varied in multilingual language experience and reading aptitudes, including both typical (TRs) and dyslexic readers (DRs). Using multivariate Partial Least Squares correlation, we identified a main component linking cognitive, linguistic, and phonological measures to brain areas underlying lexico/semantics, combinatorial processing, and amodal semantic processing. A second analysis excluding DRs showed closer associations between cognitive/linguistic, literacy, phonological and memory processes within the same brain network as in the full sample. Here, we also isolated additional, complementary components, including one involving speed, automatization and lexical access, linked to auditory and motor brain areas. This suggests greater coherence and more integrated, 'expert' processing in TRs. This work is a first step in exploring complex relationships between language and non-linguistic functions that are important to it.

KEYWORDS

Language, Cognition, Brain-Behaviour Relationships, Dyslexia, Bilingualism

1. INTRODUCTION

Language learning and use are complex, multi-component processes, yet most individuals acquire a first language (L1) and use it effortlessly. However, individual differences in L1 processing exist not only in children but also in adults (for a review, see Kidd et al., 2018), even though in adults, language skills and processing are usually thought to be consolidated and at the highest, 'ceiling' performance levels. Variability amongst native speakers has been demonstrated in different linguistic domains, for example in grammatical abilities (Dąbrowska 2012; Dąbrowska 2018), speech fluency (Mulder and Hulstijn 2011), vocabulary and lexical knowledge (Mulder and Hulstijn 2011; Dąbrowska 2018), the consistency of native phoneme production (Kartushina and Frauenfelder 2014) and sentence comprehension (Vuong and Martin 2014; Engelhardt et al. 2017). This variability is also found in language aptitude, the potential for second language (L2) learning (Wen et al. 2017).

Language skills are also linked to domain-general cognition, and the interaction between different language domains and cognition contributes to the highly variable profiles between individuals (Kidd et al. 2018). Some examples include the heavy reliance of language on working memory processes (Wen 2012; Singleton 2017; Feng et al. 2021), the comprehension of complex input being mediated by domain-general executive control abilities (Vuong and Martin 2014; Engelhardt et al. 2017) and lexical and grammatical processes being supported by general declarative memory processes and procedural memory mechanisms, respectively (Ullman 2004; Ullman 2016).

Domain-specific skills such as motor abilities, musicality and numerical skills have also been shown to interact with language. Early development of motor skills has been associated with

faster language development in children (Libertus and Violi 2016; Gonzalez et al. 2019). This association might be due to the fact that better motor skills, for example the ability to sit, are associated with more active participation in language and communication (Libertus and Violi 2016), but also because of the presence of common underlying mechanisms subserving both verbal (i.e. oral) and nonverbal (i.e. sitting) motor control (Alcock and Krawczyk 2010). Musical skills have also been shown to interact with language skills. Language and music share a number of features: both rely on symbolic systems to convey information through the auditory channel, are governed by combinatorial rules, and they partially share their genetic underpinnings (Nayak et al. 2022). In the clinical domain, musical interventions targeting auditory and attentional skills have been successfully used to remediate dyslexia (Rolka & Silverman, 2015)(Rolka & Silverman, 2015).

Arithmetic and numeracy, i.e. informal mathematical skills not requiring symbols and predictive of mathematical development (for an overview see Purpura & Lonigan, 2013), is another kind of domain-specific skill that interacts with language. Numeracy and language both rely on processes such as working memory and executive functions. The phonological processes that underpin language and reading have an impact on the ability to perform mathematical operations that rely on the rehearsal of verbal information (Simmons and Singleton 2008). Mutual relationships between language and early numeracy already exist in pre-schoolers (Purpura and Napoli 2015), with early mathematical abilities shown to be mediated by early mathematical language (e.g. mastering of words such as ‘more’, ‘fewer’, ‘count’; Toll & Van Luit, 2014). Finally, dyslexia, which affects reading and phonological processes, and dyscalculia, a deficit related to the use of numerical information and the learning of mathematics, often co-occur and share common genetic risks (van Bergen et al. 2023).

Both functional and structural neuroimaging studies have uncovered neural differences underlying individual variation in key language processing and learning abilities. For example, neural correlates have been revealed for foreign speech sound production (Golestani and Pallier 2007), foreign speech sound discrimination (Golestani and Zatorre 2004; Golestani et al. 2007; Turker et al. 2018; Turker et al. 2019), vocabulary knowledge (Lee et al. 2007) and grammar learning (Kepinska, Pereda, et al. 2017; Kepinska, Rover, et al. 2017; Kepinska, de Rover, et al. 2017; Kepinska, de Rover, et al. 2017; Kepinska et al. 2018). Other works have explored the relationship between language-specific and other domain-general skills tested using a wide set of tasks (Hintz, McQueen, et al. 2024; Hintz, Voeten, et al. 2024), with some papers exploring the interaction between cognition and language in relation to different neural correlates (Turker et al. 2017; Turker et al. 2019; Feng et al. 2021; Ramoser et al. 2024). However, a comprehensive multivariate investigation relating not only language-specific skills but other cognitive and domain-specific skills to brain functional activation during language tasks is, to our knowledge, still lacking.

In the present work, we explored multivariate brain-behavioural associations between a broad range of behavioural tasks with individual brain activation during L1 speech listening, in part using data from a recently acquired dataset (Rampinini et al. 2024 Aug 28). Activation for speech in the native language has been shown to remain stable over time, as shown by participants scanned using a similar localizer paradigm as in this study, with an average interval of 8.5 months between scans (Mahowald and Fedorenko 2016). The extent of activation of the language network is also related to multilingual language experience, with polyglots activating the same traditional perisylvian language regions as multilingual speakers, but to a lesser extent (Jouravlev et al. 2020). Further, brain activation for L1 is thought to partially overlap with that for L2,

although some dissociations are found, particularly at lower proficiency levels (Sebastian et al. 2011; Cao et al. 2013) and at later ages of acquisition (Liu and Cao 2016). Better L1 skills are predictive of higher coactivation for printed and spoken language (i.e. print-speech convergence; Marks et al., 2019), shown to underlie more successful reading development (Shankweiler et al. 2008; Preston et al. 2016; Marks et al. 2019). Moreover, L1 neural responses have been found to be partially predictive of L2 learning skills (Díaz et al. 2022; Fuhrmeister et al. 2023). Given that neural activation for L1 language processing has been associated with individual differences in L2 outcomes, in reading skills, in multilingual experience and/or in predisposition, it can be considered to be a good indirect marker for individual differences underling these aspects of language skill and experience.

Here, we explore the overarching, complex relationship between language, cognition, and non-linguistic domain-specific skills, and brain activation for native language speech processing. Previous work has explored the behavioural associations between different domains (Hintz et al. 2020; Berthele and Udry 2021; Rampinini et al. 2024), and a wealth of publications have investigated the neural underpinnings of individual (or of a smaller number of) language abilities. However, less work has been done to explore key dimensions supporting language processing beyond language-specific skills and their corresponding neural correlates in a multivariate way. Although recent work has started to highlight the importance of multimodal and multivariate analyses of language learning profiles, this approach remains relatively underexplored (Feng et al. 2021). In the present study, we collected data from a relatively large participant sample (n = 152) on behavioural measures of language, cognition, musicality, arithmetic and motor skills, as well as on measures of language and reading experience. Moreover, brain activation for speech in their L1 was collected during a story listening task. Participants varied broadly in terms of their

multilingual language experience, with knowledge of 1 to 26 languages, and in terms of their reading aptitudes, with the inclusion of both typical and dyslexic readers. Here, we leverage the variability of our participant sample and of the wide array of behavioural data to uncover, in a data-driven way, the associations and dissociations within and between each data type (i.e. brain and behaviour). We use Partial Least Squares correlation (PLS), a method that identifies components that explain shared variance between two data types, to uncover this relationship. We aim to shed light on convergences and divergences between the main cognitive dimensions related to language processing, and their relationship with neural activation for speech.

2. METHODS

2.1. Stimuli and procedure

2.1.1. Participants

152 participants took part in the study. Participants were healthy, mostly speaking French as a first language and having knowledge of two or more languages. None of the participants had official qualifications for language translation or interpretation, nor did they have professional musical training. Participants who spoke more than 6 languages were included in the study even if French was not their native language, if they reported advanced French proficiency. Figure 1 depicts the multilingual background of the participants in the sample included in the analysis, TRs had on average higher multilingualism scores than DRs (as shown also in the Supplementary results). Details of the participants' language and demographic backgrounds are available in the supplementary materials (Table 1). The final sample only included participants who did not have missing data on any of the measures analysed. It consisted of 134 participants, aged between 18.1

and 47.2 years (*M* = 24.0, *SD* = 4.9, 92 females). A subset of these participants (*n* = 25) was diagnosed with dyslexia before taking part in the study. A second analysis was run only on 109 typically reading participants (TRs), again selected based on having no missing data. In this subsample, participants were between 18.2 and 47.2 years of age (*M* = 24.1, *SD* = 5.07, 74 females).

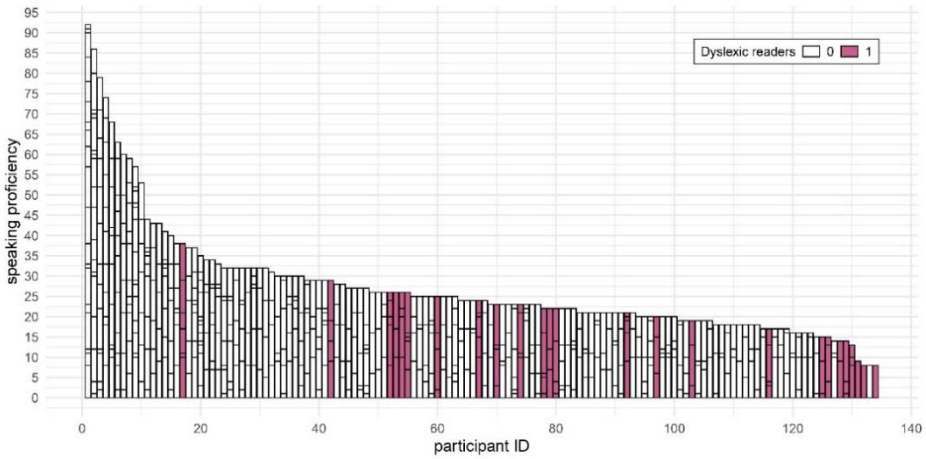

Figure 1. Language background of the participants in the sample. Each bar represents the language experience of one participant; the height of the stacked bars within each bar represents the self-reported speaking proficiency for individual languages (the taller the bar, the higher the speaking proficiency for that language). Before plotting, the data was sorted based on cumulative language experience values; as a result, the left-hand side of the figure displays hyperpolyglots' data while the right-hand side shows data from monolinguals. Dyslexic readers are marked in dark pink.

2.1.2. Procedure

Each participant took part in 4 different sessions (spread over several testing days): session 1 to fill in online questionnaires, session 2 to perform a portion of the tasks online while supervised

by one trained member of the team, session 3 to complete in-person tasks that required closer supervision or standardized hardware and session 4 for neuroimaging and genetic data collection (the latter not included in this study). Questionnaires (session 1) were delivered using Qualtrics XM©, online tasks (sessions 2 and 3) were delivered using Gorilla, and the fMRI task (session 4) was presented using Psychtoolbox3 (Matlab r2021b). An overview of all the tasks and behavioural measures are presented in Table 1. Detailed description of the hardware, procedure, and extended descriptions of the behavioural tasks and their references can be found in (Rampinini et al. 2024). All eligible participants provided signed informed consent for all subsequent experimental procedures and data reuse. The study received ethical approval from the Geneva Cantonal Ethical Commission (Protocol N. 2021-01004).

2.1.2.1. fMRI data collection

All participants took part in an MRI session where we collected brain structural (MPRAGE), MP2RAGE, DWI) data, and functional imaging data during resting-state, and during music, reading and language localizers, the latter both in the participants L1 and L2. In this work, we only analysed fMRI data from the language localiser in the L1, and used the T1 MPRAGE sequences for co-registration. Images were acquired using a Siemens 3T Magnetom-Prisma scanner at Campus Biotech (Geneva), equipped with a 64-channel coil. T1-weighted MPRAGE structural images were collected using 208 sagittal slices (TRs = 2,300 ms, TE = 3,26 ms, voxel size: 1×1×1 mm;). BOLD activation was measured using a whole-brain EPI sequence (acceleration factor -1, FOV=224 mm, voxel size: 2×2×2 mm, TRs = 2000,0 ms, TE=32,00 ms flip angle 75 □, interleaved acquisition, 72 slices).

During the fMRI task, participants passively listened to intact and degraded speech passages of the story 'Alice in Wonderland' while fixating a black fixation cross on a white screen. The stimuli and task are openly available (http://web.mit.edu/evlab/aliceloc/index.html), and the procedure for the degradation of low-level auditory features is described in Malik-Moraleda and colleagues (2022). We used the localiser to present intact and degraded passages for both the L1 and the L2 to each participant. In total, 3 runs were acquired, each including 5 fixations blocks of 12 seconds and 16 blocks of 18 seconds each, 4 per each of the intact and degraded conditions. No response was required, and participants took short, self-timed breaks between blocks.

2.2. Analysis

2.2.1. Behavioural data

Behavioural data for the questionnaires and the tasks completed on the Gorilla online platform were analysed and scored using in-house Python scripts. Tasks requiring manual scoring, such as spelling or foreign language imitation, were scored manually by native speakers. All measures, with their corresponding tasks and scores, are outlined in Table 1. A more detailed description of the behavioural tasks, together with descriptive results and reliability indices for each task, can be found in Rampinini and colleagues (2024). The supplementary materials (Figure 1) include plots with scores for all participants in all of the included behavioural measures, divided by reading group.

Variable name	Task Name	Brief task description	Selected score	Domain
Reading history	AHRQ	Reading experience, enjoyment and familiarity with reading difficulties	AHRQ index	Language experience
Musical abilities	AMMA	Sensitivity to tonal and rhythm change	Accuracy	Domain-

				specific skills
Alerting network (ANT)	ANT-I	Ability to use an auditory alerting cue to speed the reaction to a target	RT no cue trials – RT cued trials	General cognition
Orienting network (ANT)	ANT-I	Ability to use an orienting cue to orient attention to the target location	RT incorrectly cued trials - RT correctly cued trials	General cognition
inhibition (ANT)	ANT-I	Ability to correctly report target direction irrespective of the surrounding flankers (Simon task)	RT incongruent trials - RT congruent trials	General cognition
Grammar analysis	ArtGram	Ability to infer morphosyntactic characteristics of an artificial language and translate sentences after the presentation of some examples and dictionary	Accuracy	Language skills
Artificial grammar learning	Brocanto	Grammaticality judgment of sentences in an artificial grammar after repeated presentation of grammatical examples	Accuracy	Language skills
Visual memory span	Corsi blocks	Reproducing a visuo-spatial sequence	Span (forward and backward)	General cognition
CVLT short term	California Verbal Learning Test	Ability to recall a 16-item list immediately after presentation (5 trials) and after presenting an interference list.	Accuracy	General cognition
CVLT long term	California Verbal Learning	Recognition, 20 minutes after encoding, of items memorized. Presentation of both targets and semantic and phonological distractors	Accuracy	General cognition

	Test			
Visual declarative memory	DecLearn	Ability to recognize both real and invented objects 10 minutes after incidental encoding	Accuracy	General cognition
Verbal memory span	Digit span	Short-term and working memory span for digits	Span (forward and backward)	General cognition
Foreign speech sounds imitation	Farsi uvular production	Imitation abilities for uvular sound production	Percentage of correct responses	
Finger tapping speed	Finger tapping	Tapping speed with dominant and non-dominant hands	Average tapping speed	Motor skills (speed)
Foreign speech sound discrimination	Hindi dental retroflex contrast	Adaptive task measuring ability to discriminate a dental-retroflex plosive consonant contrast	Accuracy weighted by difficulty	Language skills
Multilingualism (speaking)	LEAP-Q	Self-report of language experience: number of languages known, in what modality, manner and age of acquisition, proficiency and current exposure	Entropy scores for speaking	Language experience
Multilingualism (comprehension)	LEAP-Q	Self-report of language experience: number of languages known, in what modality, manner and age of acquisition, proficiency and current exposure	Entropy scores for comprehension	Language experience
Multilingual exposure	LEAP-Q	Self-report of language experience: number of languages known, in what modality, manner and age of acquisition, proficiency and current exposure	Entropy scores for exposure	Language experience
Motivation	MFQ	Self-report for motivation for language	Total score	Language

(attitude)		learning		motivation
Motivation (openness)	MFQ	Self-report for motivation for language learning	Total score	Language motivation
Rote learning	MLAT 5	Vocabulary learning in an unknown language	Accuracy	Language skills
Musical training	MUSEBAQ	Questionnaire on musical experience and type and amount of musical training	Musical training index	Music experience
Phoneme suppression	Phoneme suppression	Repetition of nonword removing the first sound	Accuracy	Phonological awareness
Purdue pegboard dominant	Purdue pegboard test	Test for fine motor dexterity	Average number of completed trials, dominant hand only	Motor skills (dexterity)
RAN (RT)	Rapid automatized naming	Rapid naming of objects, colours, digits	Average reaction time (all categories)	Literacy mediator
Fluid intelligence	Raven's APM	Reasoning abilities, ability to complete an incomplete pattern	Accuracy	General cognition
Arithmetic	Revised tempo test	Speeded resolution of sums and subtractions	Maximum number of completed trials	Domain-specific skills
Word spelling	ECLA16	Spelling of words after auditory presentation	Accuracy	Literacy
Pseudoword spelling	ECLA16	Spelling of pseudowords after auditory presentation	Accuracy	Literacy

Spoonerism	Spoonerisms	Ability to transpose the initial sounds of two pseudowords	Accuracy	Phonological awareness
Procedural memory	Serial reaction time	Ability to tap following the pattern visually present on screen, implicit sequence presented across 5 blocks	Procedural learning gain	General cognition
Reading text (Alouette)	Alouette	Ability to correctly read a non-sensical text passage within 3 minutes.	Accuracy	Literacy
Reading text (Pollueur)	Pollueur	Ability to correct a text passage within 3 minutes.	Accuracy	Literacy
Word reading (RT)	ECLA16, EVALEC	Reading of regular and irregular words	Average reaction time per block	Literacy
Pseudoword reading (RT)	ECLA16, EVALEC	Reading of pseudowords	Average reaction time per block	Literacy
Nonword repetition	Nonword repetition	Repetition of nonwords with increasing span length	Accuracy	Phonological awareness

Table 1. Overview of the tasks, scores and resulting variables obtained from behavioural testing. All the scores, including reaction times and other metrics used in this analysis, were transformed such that higher values consistently indicate better performance.

2.2.2. Preprocessing fMRI data

Functional images were preprocessed using FSL 6.0. Preprocessing was carried out using FEAT (FMRI Expert Analysis Tool, version 6.0) with a standard preprocessing pipeline that included the following steps: removal of non-brain tissue using optiBET (Lutkenhoff et al. 2014), B0 unwarping using fieldmap images and nonlinear registration to structural T1 images (BBR,

FNIRT), and spatial smoothing using a Gaussian kernel of 5 mm FWHM. Data were motion-corrected using ICA-AROMA (Pruim et al. 2015) and no participant had an absolute displacement higher than 5 mm (which would have resulted in their exclusion from the sample). We then removed nuisance regressors (white matter, WM, and cerebral-spinal fluid, CSF), performed high-pass filtering at 90 s and registered the preprocessed data to the MNI152 standard space (Grabner et al. 2006). The BOLD response was modelled using a double-gamma haemodynamic response function (HRF). Activation for intact and degraded L1 speech listening was modelled, and the intact *vs.* degraded speech contrast was generated.

2.2.3. Extraction of individual level activity with parcellation

Once the intact *vs.* degraded brain activation contrast was computed for each participant, we defined different brain parcels in order to maintain a whole-brain approach while reducing the numbers of brain variables for the PLS analysis (i.e. as compared to a voxel-based approach). We included all cortical and subcortical regions. For the cortical regions, a total of 397 parcels, or regions of interest (ROIs) were identified. The cortex was segmented using the Glasser multimodal parcellation (Glasser et al. 2016). The parcellation was adapted to volume space, registering it to the same MNI152 template as the functional data (Horn 2016 Jun). The volume was then split by hemisphere to obtain 180 parcels per hemisphere. In the results section, cortical ROI labels correspond to each area's name in the original parcellation publication (Glasser et al. 2016). ROIs for the hippocampus were excluded from the cortical parcellation because hippocampal areas were defined using a subcortical atlas, as follows: subcortical regions comprising bilateral hippocampus, thalamus, amygdala, pallidum, putamen, and caudate nucleus were identified using the Harvard-Oxford subcortical atlas (Makris et al. 2006). Cerebellar

regions were identified using a probabilistic cerebellar atlas (Diedrichsen et al., 2009; full list of cerebellar ROIs in the supplementary material). Both subcortical and cerebellar areas were extracted using a threshold of 50%. The full list of ROIs is presented in the supplementary materials. For each of the ROIs obtained using the above parcellations, average contrast values for the difference in brain activation for intact *vs.* degraded speech were extracted. The resulting brain dataset extracted for each participant contained the average contrast values for each of the 397 ROIs.

2.2.4. PLS

Both brain and z-scored behavioural datasets were corrected for age, sex and handedness through residual calculation before the data was input to the PLS correlation (; Krishnanet al., 2010, 2011; McIntosh & Lobaugh, 2004) analysis. We used PLS to evaluate the multivariate relationship between the two data modalities, brain and behavioural, aiming to isolate components that capture shared variance between the two sets of data. After data preprocessing and preparation, the analysis was performed using the myPLS toolbox (https://github.com/danizoeller/myPLS). A correlation matrix between behavioural and brain data was generated, and then the main components which explained the relationship between the two modalities were extracted through singular value decomposition. For each component, brain and behavioural weights were calculated: these explain how strongly each single variable contributed to the multivariate correlation between the data modalities in that component. Behavioural weights, or saliences, represent how strongly each variable contributes to the correlation between modalities explained by each component. Brain weights, or saliences, represent how strongly each ROI, in our case the average contrast values for the difference in brain activation for intact *vs.* degraded L1 speech

listening for each region, contributes to the correlation between modalities explained by each component. The significance of each component was assessed using 1000 permutations, and the stability of the weights of each variable per component was evaluated using a bootstrapping procedure (500 samples). The significance of each variable was determined using a *Z* score >=|3| threshold, which corresponds to a two-tailed probability of 0.0013. Previous work suggested that a Z score >=|2| (Krishnan et al. 2011) or >=|2.57| (equivalent to a two-tailed probability of 0.01; McIntosh & Lobaugh, 2004) could be used, but in the present analysis, given the significant number of variables used in both datasets, we chose a stricter threshold to consider the results robust/significant. The results report weight means and standard deviation after bootstrapping for each variable/ROI. More details on permutation, bootstrapping and thresholding procedures are available in the Supplementary Materials (Supplementary methods section). As mentioned in the Participant section, we initially ran the analysis on the full sample including TRs and DRs (*n* =134), and then on a subsample including TR participants only (*n*=109). We could not perform a separate analysis on the DRs alone due to their smaller sample size (*n* =25), which, given the number of variables included in the analysis, would likely have resulted in overfitting and poor generalization (Mihalik et al. 2022). To ensure that any potential differences between the two analyses were due to sample characteristics and not to differences in sample size, we ran an additional PLS analysis on a third subsample, hereafter referred to as the verification subsample. This had the same sample size as the subsample of TRs only (n=109), but included the same proportion of TRs and DRs as the full sample.

3. RESULTS

3.1. Partial least square results

Overall, the analysis on the whole sample resulted in one significant component whereas the analysis including TR participants only resulted in 3 significant components. The analysis from the verification subsample showed a substantial overlap with the results in the whole sample, confirming that differences between the latter and the TRs only sample were likely due to differences driven by sample characteristics and not sample size reduction. All the results for the verification subsample are available in the supplementary material.

3.1.1. Brain and behavioural relationships in the whole sample

We applied a PLS analysis to the 36 behavioural measures and to the average activation (contrast values for intact *vs.* degraded L1 speech) from the 397 cortical and subcortical areas during L1 speech listening. One component was significant after permutation testing (p = .006, r = .34). Figure 2 shows the contribution of each variable from both modalities to the brain-behavioural correlation component (more details are available in the Results section of the Supplementary Material). The component explained 36% of the brain-behavioural covariance

At the behavioural level, the component was mostly positively associated with half of the behavioural tasks (Figure 2A). This component identified an association between measures of general cognition (memory in particular), language skills (with a prominent role of grammar) and to a lesser extent of phonological skills. More specifically, a positive association was found between the brain measures and measures of language and cognition that rely heavily on memory processes (such as Nonword repetition, declarative and verbal memory, and Rote learning), pattern recognition and learning (morphosyntactic patterns for a grammar analysis task, and

visual patterns for fluid intelligence scores), or a combination of both (as seen in artificial grammar learning). Artificial grammar learning skills were, both in the full sample and in the typical readers only (see next analysis) the strongest contributors to the component. Another set of measures pertain to the auditory domain and to auditory working memory: musicality and phonological awareness (including spoonerisms, nonword repetition, and foreign speech sound imitation), and to a literacy measure involving sound-symbol correspondences (i.e. word spelling). Multilingualism scores, with a stronger influence of multilingual comprehension than of speaking, also contribute positively to this component. Moreover, there was a positive contribution of alerting skills, i.e. a measure of response readiness and of sustained attention to incoming stimuli (Ishigami et al., 2013), and of motor dexterity (Purdue pegboard test). Last, Multilingual exposure, differently from multilingual comprehension and speaking abilities, contributed negatively to the component, with a relatively low weight compared to positively associated variables.

All cortical and subcortical brain regions showing a significant contribution to the component, and their weights, are shown in Figure 1B (results for cerebellar ROIs and uncorrected results can be found in the Supplementary Materials). Overall, better performance on the above tasks correlated with stronger activation of bilateral anterior temporal cortical areas (e.g. STGa, STSda, STSva, TGd, TGv, TE1), posterior cingulate areas (e.g. RSC, v23abm, POS1), inferior parietal regions (PGi, PGs, PFm), and temporo-parietal-junction (TPJ; TPOJ1, TPOJ2, TPOJ3). The latter regions – inferior parietal cortex and adjacent temporo-parietal junction – showed somewhat left *versus* right hemisphere lateralization, respectively. Other areas that displayed a significant positive activation in relation to behavioural measures comprised predominantly left-lateralised dorsolateral prefrontal (8v, 8c) and inferior frontal (IFJp, 45)

regions. Better scores also positively correlated with activity in medial temporal regions such as the entorhinal cortex (EC) and perirhinal cortex (PeEC) in the left hemisphere, presubiculum (PreS) in the right hemisphere and para-hippocampal (PHA3) areas bilaterally. Subcortically, Figure 2c shows a positive correlation with bilateral amygdala and right hippocampus. None of the cerebellar regions were significantly associated with the component.

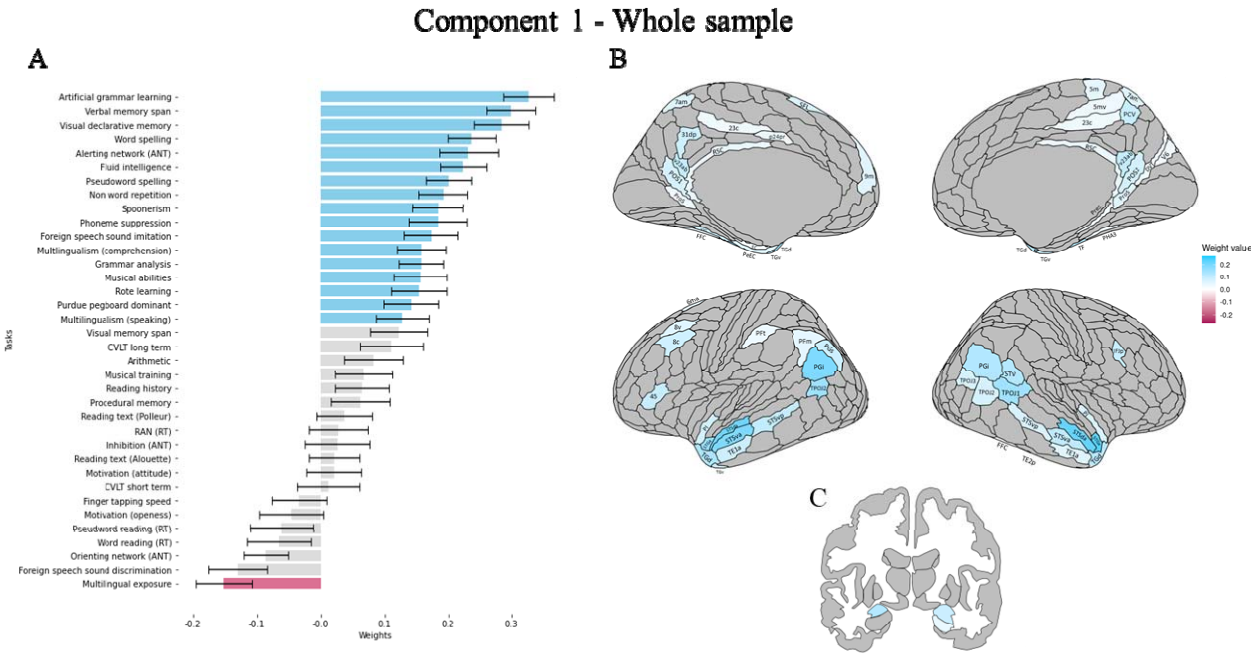

Figure 2. Results of the behavioural, cortical and subcortical saliences/weights for the significant correlational PLS component in the whole sample. Blue represents significant positive weights, red represents significant negative weights, and grey represent non-significant ones. (A) Contribution of behavioural variables to the component (for all scores, higher values represent better performance). (B) Contribution of cortical ROIs to the component. (C) Contribution of subcortical areas to the component. For each component, mean weights, SD and brain uncorrected results can be found in the supplementary material, in the Supplementary results section.

3.1.2. Brain-Behavioural relationship in typical readers only

We applied a second PLS analysis to the same behavioural and brain measures presented in the above section, but this time, we included only participants without a dyslexia diagnosis *(n* = 109). After permutation testing, we identified 3 significant components.

Component 1

The first component accounted for 44% of the variance (p = .001, r = .45). Behaviourally, this component resembles the one identified in the whole sample, but it is associated with a higher number of memory measures and, differently from the whole-sample analysis, includes a larger number of literacy measures (brain and behavioural saliences are shown in Figure 3).

A positive association was found with memory measures (such as Nonword repetition, Visual declarative and Verbal memory span, and Rote learning), pattern recognition and learning (Grammar analysis, Fluid intelligence, Artificial grammar learning), auditory measures including working memory: musicality and phonological awareness (including Spoonerisms, Nonword repetition, and Foreign speech sound imitation), and to a literacy measure involving sound-symbol correspondences (i.e. Word spelling). Positive associations were present also for multilingualism scores for comprehension and speaking, alerting skills and motor dexterity (Purdue pegboard test). Moreover, focusing on the differences in the present TRs analysis compared to that in the full sample, here component 1 was associated with additional measures for memory (CVLT long term, Visual memory span), arithmetic, literacy and literacy mediators (RAN, both Reading text measures, Reading history). Also, even though this component includes measures of phonological abilities in both the TRs and the whole-sample analyses, in this analysis including only the TRs group, the phonological measures play a more prominent role

(i.e. higher weights). This suggests a stronger influence of phonology, which is particularly interesting when considering that this component also encompasses literacy measures. Finally, in the whole sample, multilingualism exposure contributes negatively to the component.

At the brain level, the ROIs contributing to the first component were similar to those contributing to the single component found in the whole sample, with more bilateral activation especially in temporal areas. Higher behavioural scores were associated with more activity in middle-to-superior posterior (STSdp, STSdp) and anterior (STSda, STSva, TE1a, STSva, STSda, STGa, TGd, TGV) temporal areas, in frontal areas (IFJa and 45 on the left, 45 and 47l on the right), in posterior inferior parietal regions (e.g. PGi, and surrounding clusters, again predominantly left-lateralised) and in temporoparietal regions (e.g. TPOJ2), the latter again somewhat right lateralised in extent. There was also a positive correlation with medial posterior cingulate (RSC, POS1, 23ab, 31pv and surrounding areas), and bilateral presubiculum (PreS) and parahippocampal (PHA1, PHA2, PHA3) areas. Subcortically, areas that contribute positively to the relationship are the right hippocampus and left amygdala, and the cerebellum on the right crus II. All results for cerebellar ROIs and uncorrected results can be found in the Supplementary Materials.

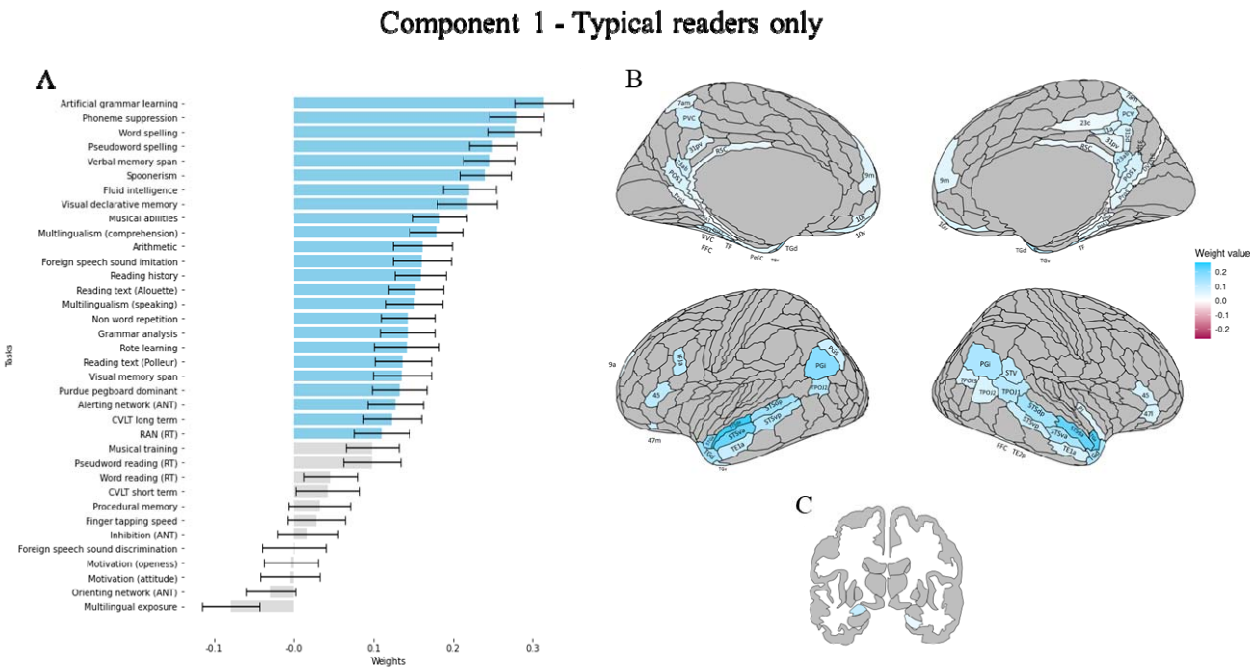

Figure 3. Results of the behavioural, cortical and subcortical saliences/weights for the first significant correlational PLS component in the typical readers. Blue represents significant positive weights, red represents significant negative weights, and grey represents non-significant ones. (A) Contribution of behavioural variables to the component (for all scores, higher values represent better performance). (B) Contribution of cortical ROIs to the component. (C) Contribution of subcortical areas to the component. For each component, mean weights, SD and brain uncorrected results can be found in the supplementary material, in the Supplementary results section.

Component 2

The second component (Figure 4) accounted for 19% of the variance (p = .012, r = .35). This component was mostly negatively associated with tasks mainly related to motor and processing speed and lexical access compared to Component 1. Negative associations were present for motor speed, with Finger tapping speed (and not for dexterity, as in Component 1) and lexical access, reading and memory (RAN, CVLT short term, word and pseudoword reading, non-sensical text reading) and phonological perception. Two tasks measuring Visual declarative memory and

phonological skills (Spoonerisms) were also positively associated with the component, with overall smaller weights compared to the negatively correlated measures.

At the brain level, mirroring the behavioural results, lower-level auditory and sensorimotor areas were associated with this second component. Poorer performance on the tasks negatively contributing to the component was associated with more activation in bilateral early auditory (A1, MBelt, PBelt, LBelt, A4, A5) and other auditory temporal association areas (TA2). Moreover, left primary motor (4) and bilateral sensorimotor cortices (areas 3a, 3b on the left, and areas 1, 2 on the right) were involved. Smaller positive contributions came from bilateral opercular/insular regions (e.g. OP4, 43, FOP1 bilaterally, OP1, RI, PFcm on the left). None of the subcortical or cerebellar ROIs contributed significantly to this second component. All results for cerebellar ROI and uncorrected results can be found in the Supplementary Materials.

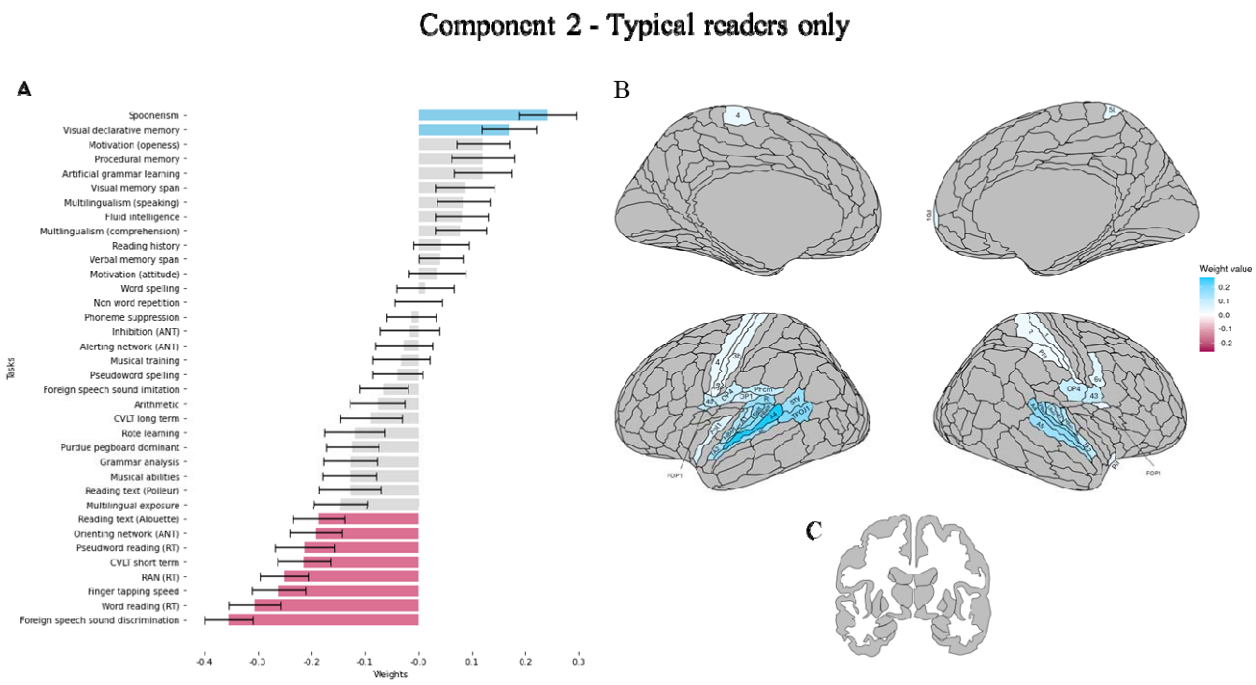

Figure 4. Results of the behavioural and cortical and subcortical saliences/weight for the second significant correlational component in the typical readers. Blue represents positive weights, red represents negative weights, and grey represent non-

significant ones. (A) Behavioural correlation for each individual variable to the component (for all scores higher values represent better performance). (B) Cortical ROI correlations with the component. (C) Subcortical areas correlations with the component. For each component, mean weights, SD and brain uncorrected results can be found in the supplementary material, in the Supplementary results section.

Component 3

The third component accounted for 8% of the variance (p = .026, r = .67). This component showed the most complex pattern of results in the analysis. Figure 5A shows that it was behaviourally negatively associated with measures of auditory and phonological skill (e.g. Nonword repetition, Foreign speech sound discrimination, Phoneme suppression) and Verbal memory span score, and positively associated with a mix of cognitive, linguistic, and multilingual experience measures, some of which are negatively correlated with the previous components (e.g. Text reading, RAN, Orienting).

In terms of relationships with brain activation, we observed a clearly lateralised pattern, mostly in higher-level language regions (Figure 5B). In the left hemisphere, regions contributing positively to the component included early auditory (MBelt, Pbelt) and associative auditory areas (STSda, STSva, STSdp, STSvp, STGa, A4, A5), as well as some clusters in opercular regions (45,43, OP4). Negative relationships were observed in right-lateralised areas such as the inferior frontal (IFJp, IFJa, IFSp, IFSa, 44, 45) and dorsolateral prefrontal cortices (55b, 8c, P9-46v, p47r), in the temporoparietal junction (e.g. TPOJ1, DTV), in the posterior STS and in other medial clusters (SFL, SCEF). In the right hemisphere, positive associations were only found with a left parahippocampal area (PHA2) and with one region in the posterior cingulate cortex (v23ab). None of the subcortical regions were significantly associated with this component

(Figure 5c), and only the left cerebellar area VIIb negatively contributed, though marginally, to the component (Supplementary material).

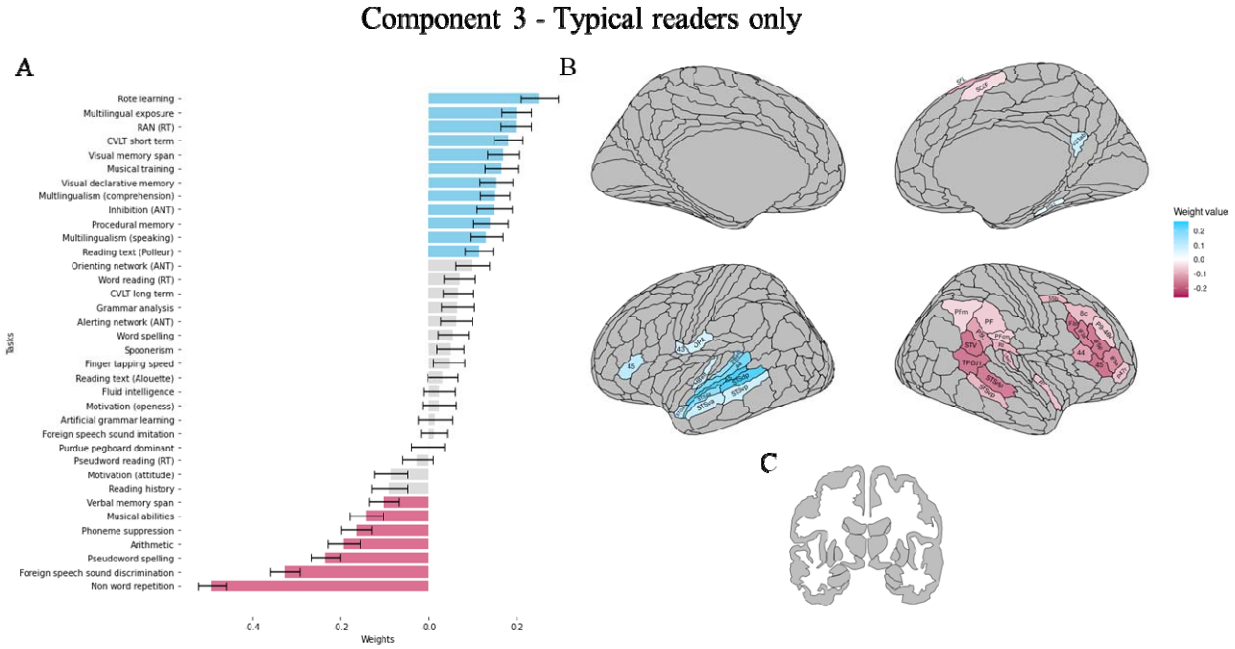

Figure 5. Results of the behavioural and cortical and subcortical saliences/weight for the second significant correlational component in the typical readers. Blue represents positive weights, red represents negative weights, and grey represents non-significant ones. (A) Behavioural correlation for each individual variable to the component (for all scores higher values represent better performance). (B) Cortical ROI correlations with the component. (C) Subcortical areas correlations with the component. For each component, mean weights, SD and brain uncorrected results can be found in the supplementary material, in the Supplementary results section.

4. Discussion

We investigated brain-behaviour associations by examining, in a data-driven and multivariate manner, behavioural measures of linguistic, domain-general and domain-specific skills and brain activation during story listening in the native language. We performed two PLS analyses, one on the full sample including typical (TRs) and dyslexic (DRs) readers, and the other only in typical

readers. The former analysis allowed us to explore brain-behaviour relationships across a wider range of performance – one which included a (language/reading) learning disorder, and the latter allowed us to determine which relationships are more likely to be observed in typical readers. Results that are consistent across the two analyses/samples are likely to reflect more stable and potentially more generalisable results. Results that differ between the two analyses/samples are likely to reflect differences arising from the additional inclusion of individuals with a previous history of reading disorder, and/or differences arising from inclusion of individuals with lower multilingual language experience, given that DRs on average has a lower multilingual language experience and exposure than the TRs.

In the next sections, we will discuss the brain-behaviour multivariate components arising from the two analyses, in light of how brain activation during speech processing is related to positive or negative relationships with subsets of tasks.

4.1. Overview of the components

4.1.1. Component 1

Behaviourally, Component 1 (accounting for 36% of the brain-behavioural covariance in the full sample, and 44% of the variance in the TRs) in both samples showed an association between higher-level cognitive and linguistic skills, particularly for memory and grammar, and phonological awareness. These were associated with neural activation in higher-level areas within the language network known to be involved in combinatorial processes, in amodal semantic hubs and in areas involved in phonological processing. In the TRs sample, behaviourally this component also included literacy measures, with a heavier involvement of memory and of phonological skills. This suggests that while language and cognitive measures are

strongly and consistently associated when only typically reading participants are analysed, literacy also becomes part of this association.

Overall, there are substantial similarities between the brain-behavioural association observed in the two analysis. In more detail, two of the tasks that positively contributed to this component reflect grammatical rule learning and knowledge (i.e. Artificial grammar learning and Grammar analysis) and pattern recognition (i.e. Fluid intelligence) skills, tasks that both reflect higher-level pattern/rule learning/recognition, arguably important components of cognition and intelligence. In fact, Artificial grammar learning was the strongest behavioural contributor to the brain-behavioural relationship. Neurally, activity in the bilateral dorsal and ventral anterior temporal lobes (ATL) was one of the strongest contributors to the brain-behaviour relationship of this component, again in both analyses. The ATL has been shown to be more active during reading of jabberwocky (sentences made of meaningless words) compared to lists of nonwords, indicating that this region is sensitive to abstract syntactic structure (Fedorenko et al. 2010; Pallier et al. 2011), and to be involved in lexico-semantic and compositional semantic processes (Hickok and Poeppel 2007). The left IFG (area 45) also contributed to this component; this area is known to support morphosyntactic processes (Hickok and Poeppel 2007) and is proposed to be involved in the semantic combinatorics (Friederici 2006; Schell et al. 2017).

The were also positive behavioural contributions of tasks that support or are related to lexico-semantic processing, such as memory and vocabulary learning tasks (e.g. Verbal memory, Rote learning and Visual declarative memory scores). Both brain imaging research and neuropsychological work on patients with stroke or neurodegeneration support the role of the ATL as an amodal, domain-general hub supporting semantic and conceptual knowledge and

memory (Lambon Ralph et al. 2010; Lambon Ralph et al. 2016; Gainotti 2017). In both analyses/samples, we found contributions of other brain areas that are also known to be amodal semantic hubs: the bilateral IPL (PGi, PGs), bilateral posterior cingulate/retrosplenial (e.g. RSC, POS1, v23ab), medial prefrontal (9m, left-lateralised in the whole sample and bilateral for TRs), bilateral parahippocampus, and subiculum areas in the right hemisphere and entorhinal cortex in the left hemisphere (Fernandino et al., 2016). The study by Fernandino and colleagues assessed cortical activation in response to 900 words having different sensorimotor properties (colour, shape, motion, sound, manipulation). Using conjunction analysis, they found activation in bilateral IPL, posterior cingulate, retrosplenial cortex, medial prefrontal cortex and left parahippocampal cortices for all semantic categories, suggesting that these regions serve as amodal hubs, where unimodal information converges. However, in contrast with their findings, the medial temporal regions that we identified via a multivariate approach were bilateral.

Another set of tasks that was positively correlated with this component pertained to phonological/auditory processing and working memory (e.g. Foreign speech imitation, Spoonerisms, Phoneme suppression, Musical abilities). These tasks contributed in both samples/analyses, but more so in the TRs analysis. These skills may partly drive the correlation with the activation in the posterior STS, known to be involved in speech and phonological processing (Hickok and Poeppel 2007; Hein and Knight 2008). Also, the relationship with phonological and language processing (imitation and multilingualism) may be driven by the activation with the IPL, a central hub in the dorsal phonological route of reading (Kuhl et al. 2020; Turker and Hartwigsen 2021). The IPL is associated with sound-based representations, supporting categorical perception of phonemes (Coslett and Schwartz 2018), perception of

ambiguous speech (Kilian-Hütten et al. 2011) working in combination with IFG areas to support phonological memory processes (Kellmeyer et al. 2013).

The prominent role of grammatical processing and of verbal declarative memory in this first component inevitably recalls Ullman's declarative/procedural model. According to this model, in our L1 the lexicon is learned through declarative memory processes and relevant neural substrates, while grammar is learned through procedural memory (Ullman, 2004, 2016). In contrast, for our L2 both grammar and lexicon are supported by declarative memory, with grammar gradually shifting to the procedural system as a function of proficiency (Ullman, 2004, 2016). The tasks associated with this component tapped into lexicon and memory for verbal items, as well as into the learning and analysis of artificial languages, which are expected to assess L2 grammar learning processes. In line with this, our results show that procedural memory (measured through a serial reaction time task) did not contribute to the component. However, the declarative-based tasks that do contribute to the component correlate positively with brain activation in areas supporting declarative processes, in combination with a set of semantic and amodal conceptual hubs. This suggests that the learning and use of novel (i.e. L2-like) grammatical rules and verbal memory may rely on declarative skills and underlying medial temporal structures, as suggested by the declarative/procedural models, but that they are additionally supported by combinatorial and amodal semantic systems.

4.1.2. Component 2

Component 2 (accounting for 19% of the brain-behavioural covariance), obtained in the analysis with TRs participants only, represents a complementary, lower-level component compared to Component 1. Behaviourally, there are negative contributions from tasks reflecting

automatization, processing and motor and processing speed and lexical access (i.e. the latter referring to how we access words that are stored in the mental lexicon) (Penolazzi et al. 2007). What appears to commonly underlie most of the tasks showing negative weights is that most require fast processing and quick reactivity (RAN, Orienting and Finger tapping speed). In terms of the brain, lower auditory and sensorimotor cortices contribute positively to this component. The negative relationship between the brain and most of the behavioural measures of this component could reflect optimisation or efficiency, with lower behavioural scores being associated with increased brain activation. There were also, however, positive contributions of Spoonerisms, measuring phonological awareness, and of Visual declarative memory to this component.

In more detail, bilateral activation of auditory and sensorimotor areas was associated with the above tasks, with a left-lateralised bias particularly in superior temporal regions and in the frontal opercular regions. Lower behavioural scores were associated with greater activation in auditory areas including the planum temporale, which are important for both phonological and orthographic processing in good readers (McNorgan et al. 2014). Moreover, greater activation was present in the TPJ, known to be important for speech-related auditory-motor association, this being a fundamental step in lexical access (Davis 2016 Jan 1) and being required in several of the tasks that are negatively associated with this component.

Most of these tasks also require speech production, which can explain the involvement of frontal opercular and motor areas. Bilaterally, the posterior frontal opercular/insular area 43 is associated with movements such as swallowing, area FOP1 is associated with imagined movements, and OP4 integrates sensorimotor information into actions (Baker et al. 2018).

There was also activation in the left motor (area 4) and sensorimotor areas (areas 3a and 3b). Areas 4 and 3b are thought to be involved in the control of hand/finger movements and in the processing of finger-specific information, respectively (Baker et al. 2018) The involvement of motor cortices is consistent with the correlation with our motor speed task. Moreover, left area 4 has been shown to be active during passage and alphabet writing tasks (Beeson et al. 2003).

4.1.3. Component 3

Component 3 (accounting for 8% of the brain-behavioural covariance), again identified only in TRs, showed a more complex pattern of associations. Behaviourally, it was positively associated with cognitive and multilingualism scores, and negatively with auditory/phonological abilities. These performances were associated with more activation in left superior temporal and some inferior frontal/opercular areas, and with less activation in right hemispheric IPL/TPj and IFG/DLPFC areas.

In particular, better memory, inhibition and multilingualism scores were associated with lower activity in the right inferior frontal sulcus regions (IFS; IFSa, IFSp, IFJa, IFJa), right middle frontal gyrus (area 8, p9-46v), right IFG (44, 45, p47r), and IPL/TPJ regions (e.g., TPOJ1, STV, PFm, PSL). The right IFS has been linked to music, reasoning, attention (Ruland et al. 2022) and to rule implementation (Demanet et al. 2016). The right middle frontal gyrus has been shown to be involved in attention re-orienting (Japee et al. 2015), and its connectivity to be negatively correlated with numeracy (Koyama et al. 2017), which is also negatively associated in this component. Moreover, the right IPL/TPJ region supports executive functions (including working memory and inhibition) (Rothmayr et al. 2011; Igelström and Graziano 2017) and together with right IFG areas it is part of the ventral attention network, underlying bottom-up attentional

processes (Corbetta and Shulman 2002; Igelström and Graziano 2017). At the same time, in this component, better scores on these tasks are also associated with poorer phonological awareness/musical abilities, and with greater engagement of left lateralized, early auditory (A5, A4, Pbelt, Mbelt), auditory association (STSda, STSvp, STSdp) and opercular areas (43, 45, OP4).

The relationships within this component suggest that increased multilingualism is associated with better short- and long-term memory for words and with better attention, but with poorer phonological awareness and poorer performance on tasks requiring working and short-term memory for sublexical (i.e. phoneme-level) information. This may be partly explained by the nature of our sample. Some of the most multilingual speakers (poly- and hyperpolyglots) in this study were highly proficient but non-native French speakers. Although the hyperpolyglots did not differ from the other participants in their behavioural scores on these tasks (as shown in the supplementary results, Table 10), the fact that they were listening to stories and performing tasks in a non-native language may have led some of them to rely more on lower-level auditory (e.g. acoustic) processes and on greater engagement of lower-level auditory regions to perform tasks requiring subtle phonological manipulations. Moreover, within this third component, higher multilingual experience is associated with clear brain functional lateralisation, suggesting greater engagement of a left-lateralised higher-level auditory (i.e. belt and parabelt regions including STS subregions and inferior frontal (i.e. BA 45) language network, and lower (maybe optimised) engagement of right-lateralised attention and executive areas. It should be noted, however, that this third (and last) component explains a smaller percentage of the variance (8%) compared to the other two (63% in total), and that therefore these results and interpretations may not be representative of broader and generalisable trends.

4.2. Stable associations and differences across samples

Across both samples we have shown that, at the behavioural level, cognition and language mostly overlap, suggesting a stable association. In both samples, measures including memory and grammar learning abilities were strong drivers of the brain-behavioural association in the first, most important component. Although language-specific processes at both the brain and behavioural levels can be clearly dissociated with finer-grained analyses, and although the language network has previously been shown to be less responsive to cognitive demands (Fedorenko and Varley 2016; Fedorenko et al. 2024), language does not occur in a vacuum. Language and cognitive processes interact during language learning, with changes in one domain influencing other, higher-level skills that develop later (Kidd et al. 2018; Kidd and Donnelly 2020). Moreover, language is mostly used in interaction with other individuals (Levinson and Holler 2014). This requires us to engage in other cognitive processes beyond simply retrieving semantic and syntactic information in order to keep track of the narrative, of turn taking and of conversation (Hasson et al. 2018).

At the brain level, the identified regions are areas known for supporting lexico-semantic, combinatorial, and phonological processes, and as amodal semantic hubs (particularly in typical readers only). In other words, the first multivariate component explaining most of the brain-behaviour covariance corresponds to a higher-level language network known to support semantic and combinatorial processes, as well as grammatical, mnemonic and partly phonological skills.

The differences between the analysis in the full sample (i.e. including the DRs) and the analysis including only the TRs shows that in the latter, these cognitive and linguistic processes are also associated with measures of literacy, particularly for reading fluency and history, while

also showing a stronger role for phonological awareness skills (accompanied by more STG activation). This may suggest that in typical readers, literacy skills may rely on, or be more strongly linked to, more general cognitive/linguistic behaviours and their associated high-level neural mechanisms, reflecting a more specialised, reading-ready cognitive architecture. On the other hand, in dyslexic readers, these literacy tasks may engage different brain areas, perhaps as compensatory or more variable neural activations. Moreover, it suggests that when TRs only are considered, spoken language and literacy skills (along with phonological mediators) are associated to overlapping neural substrate in this component. This finding is in line with the print-speech convergence hypothesis, which postulates that successful reading is supported by strong overlap between the neural substrate processing written and spoken language (Shankweiler et al. 2008; Rueckl et al. 2015; Preston et al. 2016).

The association between language/cognitive scores and literacy may be unexpected given previous work by our group in which we modelled data from the same dataset using exploratory graph analysis to explore the network of relationships between our behavioural scores (Rampinini et al. 2024). In this previous work, both in the full sample and in TRs only, literacy measures tended to consistently cluster separately from other language/cognitive scores. However, we need to consider that the analysis methods used were different and that here, we explored the shared variance and relationship between different data types, i.e. brain and behaviour, and not just between variables within one modality. We must consider that "cognitive processes and neural processes are not the same thing" (Valian 2016), and that while literacy tasks can be dissociated from other language/cognitive skills at the behavioural level, they could rely on mostly shared underlying neural substrates.

Finally, multilingualism exposure contributes negatively to the component in the whole sample only. This negative contribution may be due to the differences between the three multilingualism variables being measured. Multilingualism exposure assesses the number of languages currently present in the participants' environment, whereas the other two scores — Multilingualism (speaking) and Multilingualism (comprehension)—better capture language knowledge. The participants showed considerable variation in this respect, with some polyglots speaking or understanding more than 10 languages. As a result, the current exposure measure may be less informative, as polyglots might not be exposed daily to all the languages they know. In contrast, less multilingual participants (amongst which we can find DRs) are likely exposed to multiple languages daily due to the multilingual nature of the region where data collection took place. Hence, whereas multilingualism speaking and comprehension scores are highly positive associated, exposure represents an anomaly, since we can have very multilingual speakers having relatively low current exposure, which makes this measure less informative. This could explain why only language knowledge, represented by measures assessing cumulative experience with speaking and understanding one's languages, are positively related to linguistic and cognitive skills. Conversely, current exposure to language, which provides a snapshot of the language environment at the time of assessment, does not show the same relationship. Once DRs are removed, multilingual exposure remains negatively associated with the component but not significantly, possibly indicating the reduced variability between these three measures given that DRs are less multilingual.

4.3. Additional components for language in TRs only

When DRs were removed from the sample, more components explaining the common variance between brain and behaviour were identified. Particularly, Component 2 identified tasks linked to

phonological perception, speed of access to lexical items, naming speed and reading of items without the support of predictive processes, for example word reading and non-sensical text reading. This component is likely driven by the superior skills of TRs on these specific tasks. In the full sample we were not able to identify this component, probably due to the poorer or more variable performance of DRs that were included in the analysis, and due to the likely activation of additional compensatory areas involved in these processes in DRs (Kuhl et al. 2020). Such compensatory processes and brain regions may have increased the variability in the data, thereby making it harder to extract other components. This suggests that while most features of Component 1 represent more generalisable associations between brain-behavioural relationships, the variables and areas associated with Component 2 represent an important building block of language functions for the typical reading population, but do not cover the full range of variability at least when it comes to developmental dyslexia. Component 3 also represents a less generalisable trend, probably due to the inclusion of polyglots in our samples.

5. CONCLUSIONS

In this paper, brain-behaviour associations for language-relevant skills and speech processing were investigated using PLS correlation analysis. Participants with different levels of multilingual experience and reading ability were included, and the analyses were performed first on the whole sample and then on a subset of TRs only, to explore which associations were stable and which were modulated by the presence or absence of DRs.

Overall, in both samples, a main component including cognitive, linguistic and phonological measures was found to be associated with cortical areas involved in lexico/semantics, combinatorial processing and amodal semantic areas. Analyses excluding DRs

suggest that literacy and phonological processes may be more closely associated with language and cognition in TRs than when DRs are included in the sample, pointing to more shared neural resources between these processes in TRs. Furthermore, results from TRs only indicate that additional components can be identified in populations without reading deficits, in particular, a complementary component involving processing and motor speed, automatization and lexical access that is supported by auditory and motor brain areas.

This work is a first step in exploring complex relationships underlying language use and learning and domain-general and domain-specific non-linguistic skills in a multivariate way. We believe that language, as a multifaceted and multicomponent ability, should be studied comprehensively, that it should include broad behavioural characterisation of speakers and that it should ideally explore the relationship between different data modalities (e.g. brain function and structure, functional and structural connectivity, genetics, etc.). We believe that this approach can advance our understanding of language, of how individual differences arise and of how different abilities interact, and hope that future work will continue to unveil new aspects of these complex relationships.

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7. AUTHORS' CONTRIBUTIONS

Conceptualisation, I.B., A.R., O. K, R. B., N.G.; Data curation and preprocessing, I.B., A.R. and O.K.; Methodology, I.B.; Visualisation, I.B.; writing—original draft preparation, I. B.; writing—review & editing, I.B., A.R., O. K, R. B., N.G, funding acquisition, R.B and N.G.

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9. SUPPLEMENTARY MATERIALS

Supplementary materials are openly available at the project's Open Science Framework page at https://osf.io/4zcn2/?view_only=f1f5f11ba91c4e168e5321a198b4dc7a

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