Big Questions

BQ 1-4 \rightarrow November 2016 BQ 5 \rightarrow April 2019





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PREAMBLE

Preamble Big Questions team science Language in Interaction

This document contains the elaborated proposals for the Big Questions that the *Language in Interaction Consortium* has identified as the core of its research efforts for the coming years.

Implementation of these Big Questions has commenced and is an exercise in team science, an item that is of increasing importance in the academic world. Instead of small-scale individualized projects, the challenge is to try out forms of collaboration that find their reward in the answers that are provided instead of the personal claims to fame that can be harnessed. This requires team spirit and willingness to seek common ground, while at the same time keeping the big picture in mind and big questions in the foreground. The unique contributions that we can make jointly is what should drive us. It certainly comes with new challenges. But challenges of the future are not necessarily best matched with the recipes of the past.

I'm confident that we will manage to make progress in this exciting endeavour.

Peter Hagoort

Program Director

BIG QUESTION 1

1. Big Question coordinator: Dr. Stefan Frank

2. Title of the Big Question

The nature of the mental lexicon: Bridging neurobiology and psycholinguistic theory by computational modeling.

3. Key words

Mental lexicon; Neurobiological models; Vector representations; Neural encoding and decoding

4. Scientific summary of research proposal

The big question this project addresses is how to use computational modeling to link levels of description, from neurons to cognition and behavior, in understanding the language system. We focus on the mental lexicon and aim to characterize its structure in a way that is precise and meaningful in neurobiological and (psycho)linguistic terms. We will take advantage of recent progress in the understanding of modelling realistic neural networks, improvements in neuroimaging techniques and data analysis, and developments in accounting for the semantic, syntactic and phonological properties of words and other items stored in the mental lexicon. Using one common notation: high-dimensional numerical vectors, we will integrate neurobiological and computational (psycho-) linguistic models of the mental lexicon and develop methods for comparing model predictions to large-scale neuroimaging data. Our overarching goal is to devise causal/explanatory models of the mental lexicon that can explain neural and behavioral data. This will significantly deepen our understanding of the mental lexicon, lexical access, and lexical acquisition.

5. Composition of the project group

Name and title	Specialisation	Institution	Lil Work Package	Involvement
Prof. Rens Bod	Computational linguistics & Digital humanities	ILLC	3	BQ1L, supervision
Prof. Peter Desain	Brain-computer interface	Donders	7	utilization
Prof. Mirjam Ernestus	Speech comprehension, Psycholinguistics	CLS	1	BQ1P, supervision
Dr. Hartmut Fitz	Neurobiological modeling, Psycholinguistic modeling	MPI	3	BQ1N
Dr. Stefan Frank	Cognitive modeling, Psycholinguistics	CLS	tenure track	BQ1P, BQ1D, supervision, coordinator
Dr. Marcel van Gerven	Machine learning, Computational neuroscience	Donders		BQ1L, BQ1D supervision
Prof. Peter Hagoort	Neurobiology of language	MPI Donders	1	BQ1N

List of consortium members of the project group

Dr. David Neville	Concept learning	Donders	2	BQ1N
Dr. Karl Magnus	Neurobiology of	MPI	3	BQ1N, supervision
Petersson	language,	Donders		
	Neurobiological			
	modeling			
Prof. Antal van den	Computational linguistics	CLS	7	utilization
Bosch				
Dr. Willem Zuidema	Cognitive modelling,	ILLC	tenure track	BQ1L, BQ1N, supervision
	Computational linguistics			

List of non-consortium members of the project group

Name and title	Specialisation	Institution	Involvement
Dr. Jakub Szymanik	Formal semantics	ILLC	BQ1L
Dr. Raquel Fernández	Computational semantics	ILLC	BQ1L, BQ1P
Dr. Ivan Titov	Bayesian Modelling, Deep learning, NLP	U. of Edinburgh	BQ1D
Dr. Louis ten Bosch	Models of speech perception	CLS	BQ1P
Dr. Roel Willems	Neurobiology of language	CLS	BQ1D

6. Description of the proposed research within the Big Question

Introduction

One of the central challenges in the cognitive sciences is to link different levels of description, from neurons to observable behavior. The fact that this challenge remains unsolved makes it extremely difficult to use findings at one level to constrain theories formulated at another level. Hence, linguistic theory has so far paid little attention to research findings on the neurobiology of language and vice versa. This is unfortunate, because neuroscientific evidence could play a major role in resolving longstanding issues in linguistics about the nature and origins of the representations and computations subserving language processing and language acquisition. Likewise, neuroscience could benefit from a deep understanding of language - a system that exploits the computing resources of the human brain, and thus must reflect many of its properties. We feel the time is ripe to make a fresh attempt at linking these levels of description, building on recent developments in computational neuroscience, as well as recently developed machine learning techniques to explore the space of possible representations for natural language, informed by linguistic insights but without committing to only one of its formalisms.

To delineate our project, we follow a long tradition of viewing the human language system as composed of two core components: a mental lexicon stored in long-term memory and a real-time combinatorial process that combines representations retrieved from the mental lexicon. We will focus on the former. Although important differences between (psycho-) linguistic theories of language can be traced back to different views concerning the nature of the mental lexicon, there is consensus that the mental lexicon contains a considerable amount of knowledge about the phonology, combinatorial properties (morpho-syntax and semantic compositionality), and lexical semantics (e.g., Steedman, 2000; Jackendoff, 2002). Our main objective is thus to characterize the structure of the mental lexicon in a way that is meaningful in neurobiological and (psycho-) linguistic terms. We integrate neurobiological and computational (psycho-) linguistic models of the mental lexicon, we link these

models to large-scale neuroimaging, psycholinguistic and corpus data, aiming to uncover neurobiologically plausible representations and processes that support the mental lexicon.

A successful simulation of the neural processes and representations involved in long-term storage, word recognition, and lexical development will answer important questions including: What are the retrieval cues in neurobiological terms that allow long-term memory activation (lexical retrieval) to take place? What is the structure of word representations stored in the mental lexicon and how do these enable combinatorial sentence-level processing in biological networks? What kinds of representations are supported by the underlying neurobiology and how are these encoded in long-term memory? How is a mental lexicon acquired given the weak, local neurophysiological learning mechanisms available? What is the role of innate structure in the acquisition process?

Approach

The project will comprise three main research strands, respectively focusing on models of lexical representation, models of neural processing, and methods for bridging between model predictions and neural data. The results of Mitchell et al. (2008), which demonstrated that vectors obtained by methods from distributional lexical semantics can be used to predict neural responses to particular stimuli measured by fMRI, strongly suggest that bridging the different levels of description addressed in the current proposal is feasible with the computational methods we aim to apply. A key part of our approach is that we use high-dimensional numerical vectors as the common representation of lexical knowledge throughout the project. From a neurobiological point of view, it is clear that the outcomes of lexical retrieval are patterns of neocortical activity that are naturally described as evolving state vectors (i.e., not static, but dynamic patterns). Also from a machine learning perspective, such vectors are uncontroversial, as many of the successful models that deal with language data represent lexical semantic information in this way. Importantly, we also aim to use high-dimensional vector representations to encode the perceptual and combinatorial properties of words and other stored items¹. Recent theoretical work (Kanerva, 2009; Coecke et al. 2013) and empirical work (Socher et al., 2013; Le & Zuidema, 2015; Bowman et al., 2015) suggest that such vectors, and the mathematical operations that are naturally defined on these vectors, can do the same work that symbolic representations in linguistics were developed for. This provides us with the best of two worlds: a way to characterize knowledge associated with a lexical item using the same representational format as used to describe lexical and neurobiological properties, while maintaining the expressivity of the linguistic formalisms.

If a set of vectors is taken to instantiate a theory of representation in the mental lexicon, the qualities of alternative vector sets need to be evaluated. In order to do so, we intend to combine the representation models with neurobiologically motivated models of lexical access that simulate neural processing over the course of word recognition. In addition, we compare quantitative model predictions to high-resolution and large-scale data from imaging experiments.

In the current project, experts on all of these aspects come together. We thus aim to tackle the Big Question from three directions: (i) by investigating which vector representations of items in the mental lexicon are appropriate to encode their linguistically salient (semantic, combinatorial, and phonological) properties; (ii) by developing neural processing models of access to, and development of, the mental lexicon; and (iii) by designing novel evaluation methods and accessing appropriate data for linking the models to neuroimaging and behavioral data. Thus, BQ1 will integrate questions of a Linguistic (L), Psychological (P), Neuroscientific (N), and Data-analytic (D) nature.

¹ Throughout this proposal, the term 'word' refers to any item stored in the mental lexicon.

Representing items in the mental lexicon

We will focus on two extensions to the standard distributional semantics models that aim to capture combinatorial and perceptual properties of words, mainly focusing on questions of a linguistic and a psychological nature, respectively. Although a few suggestions for such extensions are present in the literature, these are not yet grounded in psychologuistic or neurobiological theory or data.

One key question (**BQ1L**) is how vector representations should be adapted to make them encode the combinatorial properties of words. What should the vector representation be for function words (prepositions, determiners, pronouns, quantifiers, conjunctions)? How can vectors encode that words occur in certain contexts but not in others? How can vector representations be used to encode the difference between transitive and intransitive verbs? To answer these questions, we will take our inspiration from syntactic and semantic theory and from computational (psycho-) linguistics, and use modern machine learning techniques to discover vector representations and composition functions that encode the required information (Socher et al., 2013; Baroni & Zamparelli, 2010; Le & Zuidema, 2015).

Current vector-space models compute vector representations for words based on the words they co-occur with in a sentence or a document (context words), typically ignoring the hierarchical structure of the sentences in which they occur (although they do pay attention to the distance between a focal word and a context word and sometimes to whether the context word appears before or after the focal word). This is in contrast to all major frameworks in theoretical linguistics, where word representations also include information about the combinatorial properties of words. Most of these frameworks are heavily lexicalized, meaning that (almost) all information needed to distinguish one natural language from another is stored within the representations of individual words (and other stored items). Thus, the representation for the word "two" contains information about its lexical semantics (it's more than 1 and less than 3), but also about its syntactic, compositional and pragmatic (as well as phonological) properties (e.g., it can turn a noun like "people" into a plural quantifier phrase that as subject requires a plural verb and may or may not have semantic scope over the object, as in "two people sing a duet" vs. "two people eat an apple"). In BQ1L we investigate how the vector representations for words can be enriched in ways that do justice to such insights from linguistics, while keeping the representations compatible with the studies carried out in BQ1P, BQ1N and BQ1D. We will approach this challenge by looking both at formalisms (the "abstract route") and at linguistic case studies (the "concrete route"). In the abstract route (BQ1L PhD) we take inspiration from the computational and formal properties of existing linguistic frameworks. We will train neural language models, using existing treebanks and other corpora, to implement or approximate these properties. Formal linguistic properties of interest include, in the first place, the ability to represent tree structure, variable binding (also known as unification, substitution or application) and semantic composition, but ultimately also type raising, polarity, monotonicity, intensionality (and other concepts from the formal semantics tradition), mild context-sensitivity, predication, c-command, binding (in the G&B sense; and other concepts from syntactic theory). The goal of these investigations is to produce a series of lexicons (words and their vector representations) that reflect increasingly sophisticated types of information about the combinatorial properties of those words. In the first study of the abstract route we will use two classes of existing models: one that takes hierarchical structure as a given (e.g., the recursive neural tensor network, the forest convolutional network) and the other where hierarchical structure may be learned (e.g., the gated recurrent network, bidirectional long short term memory networks with 'attention'). We will investigate how the second class of models can be trained to mimic the performance of the first class (currently superior on tasks where hierarchical structure is crucial), trained on treebanks such as the Penn WSJ treebank and the Stanford Sentiment Treebank. In the second study we will take the best of the models of study 1 and investigate how they can be extended to deal adequately with linguistic properties studied in richer linguistic frameworks, such as CCG and its semantic extensions (e.g., Boxer; ref. Steedman 2000; Bos, 2013). To test the limits of the neural models (and push

beyond them), we will train them mainly on artificial data generated with rich grammars such as probabilistic CCGs, which are themselves induced from treebanks.

In the concrete route (BQ1L Postdoc) we study, in machine learned vector-space models, the concrete linguistic phenomena that have motivated these properties of existing linguistic formalisms. We will start with a thorough literature review to identify the phenomena most likely to help distinguish between different neural models of hierarchical structure and semantic composition. Candidates include negation, noun-compounding, derivational morphology, agreement, determination, subsective vs. intersective adjectives, polarity, vagueness, trans-contextfreeness, island constraints, word order preferences, scrambling, fomulaic language, metaphors and many other phenomena studied in linguistics. The key is to find examples that are frequent enough to give current neural language models trained on big corpora a reasonable chance of learning good representations for them. We will then work on techniques to investigate how these existing neural models deal with the phenomena in question, and, importantly, how to quantify the performance of these models on these phenomena. In study 1 we will focus on the most fundamental 'coarse-grained' phenomena from formal semantics, starting with negation and quantifiers and the corresponding neural representations that support classical logical inference, building on the work of Socher et al. (2013) and Bowman et al. (2015). In study 2 we will look at equally foundational topics from morpho-syntax, starting with phenomena in derivational morphology and those motivating trans-contextfree structure, building on the work of O'Donnell et al. (2015) and Van Cranenburgh & Bod (2015). In study 3 we will study the more finegrained semantic and syntactic phenomena that we identify in our literature review, which might include the phenomena of polarity (a key topic in formal semantics) and island constraints (a classic topic in Chomskyan syntactic theory). In the fourth study, we will combine the insights from study 1, 2 and 3, and the PhD project, to train a rich neural model that not only learns to encode hierarchical structural properties of words where they are needed, but does so efficiently and in ways that does justice to the subtle ways in which composition works in natural languages.

BQ1L will be carried out by a postdoc and a PhD student under the supervision of Dr. Willem Zuidema (daily supervisor), Dr. Raquel Fernández (second supervisor PhD student and postdoc), Dr. Marcel van Gerven (third supervisor PhD student), Dr. Jakub Szymanik (third supervisor postdoc) and Prof. Rens Bod (promotor).

BQ1L research plan

Postdoc ("the concrete route")	Yea	ar 1	Yea	ar 2	Ye	ar 3	Year 4
Supervision and guidance of PhD project	2	Х		Х		Х	
Review of literature: linguistic phenomena, neural	Х	X					
models							
1. Coarse-grained semantics		Х	Х				
2. Coarse-grained morphosyntax				Х	Х		
3. Fine-grained semantic and syntactic phenomena						X	
4. Efficient and accurate semantic parsing							Х

PhD (the "abstract route")	Year 1		Year 2		Year 3	
Getting acquainted with literature; studying current models	X					
1. Encoding hierarchical structural in the lexicon, evaluating against imaging data		Х	Х			
2. Linguistically-rich grammars/ Artificial Data			2	X	Х	
Completing thesis						Х

Matching contributions:

1. Memory- or computation-heavy simulations will be run at the ILLC's and SURF-SARA's highperformance computing clusters.

- 1. Interaction with/integration of ongoing related PhD projects:
 - Sara Veldhoen (ILLC, supervised by Zuidema), Neural models of formal languages and logical inference
 - Dieuwke Hupkes (ILLC/Lil, supervised by Zuidema & Bod), Neurally plausible semantic parsing
 - Marco del Tredici (ILLC, supervised by Fernandez), Distributional lexical semantics in interaction

Subproject **BQ1P** aims to incorporate the perceptual features of words into the vector-space framework of the mental lexicon. This extends the current representational schemes (as well as those developed in BQ1L) with notions of auditory/phonological or visual/orthographic form. Although several computational models of word recognition make use of fairly sophisticated representations of word form (e.g., Davis, 2010; Hannagan, Magnuson, & Grainger, 2013) they are not concerned with meaning. Conversely, current distributional semantics models ignore the fact that words have phonology (and, for most people, orthography) and that the mental lexicon needs to store links between the form of words and their morphosyntactic and semantic properties. By developing continuous-valued high-dimensional vector representations of word form, in line with BQ1L's (morpho-) syntactic and semantic representations, BQ1P will facilitate modeling of the connection between form and meaning. Interestingly, the mapping between form and meaning is not completely arbitrary but displays some systematicity, for example when stress pattern provides a clue towards whether a word refers to an action (verb) or object (noun), when morphology indicated number or gender, and in case of sound symbolism. Hence, representing form is, to a limited extent, also representing meaning (Monaghan, Shillcock, Christiansen, & Kirby, 2014).

Developing word form representations may yield answers to several relevant psychological questions: Which word forms (e.g., morphological, spelling, and pronunciation variants) are stored and how are these represented? Is analogical processing a viable alternative to abstract rule application for explaining how non-stored forms are understood? What are the unique constraints posed by the properties of different input modalities (e.g., auditory versus visual presentation; static writing versus dynamic speech)? How does non-arbitrariness in the form-meaning mapping affect language processing and lexical representation?

BQ1P will be carried out by a PhD student under the supervision of Dr. Stefan Frank (daily supervisor), Prof. Mirjam Ernestus (second supervisor and promotor), with Dr. Louis ten Bosch and Dr. Rachel Fernández as additional team members. The subproject comprises three studies:

- 1. Representing written form. Using techniques developed for distributional semantics, representations are developed that map words into a high-dimensional space based on the pattern of graphemes in the words' written forms.
- 2. Representing spoken form. The insights gained from Study 1 will form the basis for a vector space model of the spoken form of words. Two additional complexities of this modality are the dynamical nature of the input signal and the large number of speech variants for the same lexical item.
- 3. Linking form to meaning. As mentioned above, word form can provide cues to meaning. Much richer semantic information is obtained by including word-level distributional information as well as non-linguistic information about the semantic/perceptual features of the words' reference.

The developed representations will be evaluated against existing behavioral data from eye-tracking experiments on reading (for Studies 1 and 3) and speech comprehension (i.e., the visual-world paradigm; for Studies 2 and 3) experiments. Further, they are compared to neural activity during comprehension in subproject BQ1D. The vector representations developed in BQ1P are related to the

neural models of phonological form from BQ1N in that they constitute an algorithmic-level description of the neural (implementation-level) representations.

BQ1P research plan

	Year 1		Year 2 Year 3		Ye	ar 4	
Getting acquainted with literature; studying current	Х						
models							
Developing and evaluating representations of written		Х					
form							
Developing and evaluating representations of spoken			Х	Х			
form							
Investigating form-meaning mapping					Х	Х	
Completing thesis							Х

Matching contributions:

- 1. Memory- or computation-heavy simulations will be run at the Center for Language Studies' highperformance computing cluster.
- 2. Interaction with / integration of ongoing related PhD projects:
 - How to slow down and speed up, the regulation of speech rate (Joe Rodd, Lil)
 - The interaction of memory-based prediction and speech register in auditory word recognition (Martijn Bentum, CLS)

Neurobiologically realistic models of the mental lexicon

In **BQ1N** we ask: What is the character of the neurobiological representation of lexical items that can support retrieval from the mental lexicon in a fashion that makes real-time, combinatorial construction of sentence-level meaning possible in the human brain? There are at least two sides to this issue. First, what are the relevant retrieval cues that allow long-term memory activation (lexical retrieval) and what is the character of the retrieved output? Second, what neurobiology supports the acquisition of a mental lexicon by encoding lexical representations in long-term memory memory and what is the role of prior, innate structure in the acquisition process? Crucially, the approach outlined below naturally captures the notions of recursive processing, context-sensitivity and compositionality (cf., Petersson & Hagoort, 2012).

Over the past three decades, computational neuroscience has provided a rich and diverse theory of plasticity principles for adaptation, learning and memory that at different time-scales, including longand short-term memory. These include mechanisms of homeostatic plasticity to stabilize neuronal and circuit activity (Turrigiano, 2012; Vogels et al., 2011; Duarte & Morrison, 2014) and a number of recent proposals locate encoding, storage, and retrieval in spike-silent dynamic processes (Petersson, 2008; Petersson & Hagoort, 2012; Stokes, 2015; Hasson et al., 2015). These processes are supported by mechanisms of short-term synaptic facilitation and depression (Markram et al., 1998; Mongillo et al., 2008), Hebbian mechanisms for long-term potentiation and depression such as spike-timing dependent plasticity (Song et al., 2000; Pfister & Gerstner, 2006; Chen et al., 2013) and mechanisms for synaptic consolidation and memory maintenance (Lisman, 1985; Frey & Morris, 1997; Zenke et al., 2015). Crucially, these have precise mathematical descriptions and a deeper understanding of how they interact at different temporal scales is beginning to emerge (Zenke et al., 2015) in order to create persistent memories (Clopath et al., 2008). These mechanisms also hold a promise to solve the stability/plasticity dilemma and avoid catastrophic interference in memory formation.

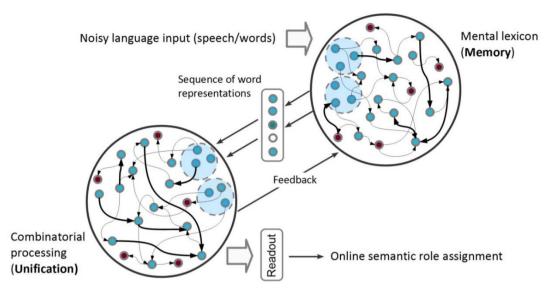


Figure 1. Cognitive architecture - spiking memory- and unification subnetworks and their interaction in retrieval and sentence-level comprehension.

The first part of this project (BQ1N PhD) will make use of these insights within the framework of spiking recurrent networks (Maass et al., 2002; Brette & Gerstner, 2005), including neurobiologically realistic connectivity (Izhikevich & Edelman, 2008) and sophisticated synapse-models (Gerstner et al., 2014), to synthesize a neurobiologically realistic model of long-term lexical storage and retrieval. The aim is to implement a model of the mental lexicon that outputs word-representations (vectors of phonological, syntactic, and semantic feature representations) that support independent, parallel access through any vector component (feature). This causal model of the mental lexicon should be capable of performing word recognition (Hopfield & Brody, 2000; Wills, 2004; Hannagan et al., 2013) and deliver lexical representations (patterns of spike-train) to a downstream, interactive unification network (Hagoort 2005; 2013) for sentence-level comprehension (Gallistel & King, 2010; de-Wit et al., 2016). The combined Memory-Unification architecture is outlined in Figure 1. The aim is to understand how neurobiological mechanisms support the linking of the input signal (retrieval cues) to vector representations of lexical items encoded in the mental lexicon during language acquisition. Model building will be supplemented by the development of analytic techniques to measure memory capacity. dynamic stability of representations, and to discover hidden representational structure in neuronal assemblies (e.g., bi-spectral clustering analysis).

The second part (**BQ1N Postdoc**) will investigate the nature of lexical representations in terms of their role in sentence processing. The network model of the mental lexicon will interactively interface a spiking Unification network (Hagoort 2005; 2013) which is currently being developed in the Neurobiology of Language Department, MPI (Fitz, Hagoort & Petersson, 2015; Fitz et al., 2016). The spiking Unification network is a high-dimensional, state-dependent processor (Buonomano & Maass, 2012) which computes sentence-level meaning over transient states (Rabinovich et al., 2008). The internal dynamics of the network is decoded onto desired outputs by calibrating simple readout networks in parallel (Rigotti et al., 2013; Singer, 2013) by similar techniques used for decoding neural activity in subproject BQ1D. Decoding can be viewed as a theory bridging between neuronal processes and psycholinguistics concepts and in this manner the unification network is able to assign, for example, semantic roles or aspects of syntax (who does what to whom) to word sequences in an online, real-time incremental fashion (Altmann & Kamide, 1999; Fitz, Hagoort & Petersson, 2015; Fitz et al., 2016). Forward projections, from the Memory to the Unification network, allow us to investigate to what extent structured word representations delivered by the mental lexicon are suitable for combinatorial processing in sentence-level comprehension. In this way it can be investigate (a) what kind of linguistic

information the unification component requires to compute in real-time an interpretation of the unfolding utterance and (b) in what representational format the mental lexicon might package this information within the neurobiological infrastructure of the human language system. Findings from these investigations will inform the subprojects detailed in BQ1L and BQ1P.

Context disambiguates words and can force unusual (Nieuwland & van Berkum, 2006) or even novel meanings onto words (Goldberg, 2006). Feedback connections from the unification network to the mental lexicon allow us to investigate the influence of context on lexical retrieval. In an integrated, neurobiologically grounded Memory-Unification network, different theoretical views on the nature of the mental lexicon (e.g., Levelt, 1989; Elman, 2004; Jackendoff, 2007) can be evaluated and psycholinguistic theories of lexical storage and retrieval can be tested in a rigorous scientific manner. The developed models will subsequently be applied to corpora of semantically annotated text (Fillmore et al., 2004; Palmer et al., 2005). This will yield insights into scalability with respect to the noisy and diverse language input that the human comprehension system has to cope with.

Common to the PhD and postdoc projects are questions of what the roles prior, innate structure might be in both networks (located, e.g., in information encoding, connectivity profile, constraints on network dynamics, decoder etc.; cf., Petersson & Hagoort, 2012) and this creates a natural link to BQ2 and BQ4.

Matching contributions

- 1. Interaction with/integration of on-going Lil PhD project "Neurobiological Models of Language Processing" (1 year in).
- 2. The costs of the MPI in-house grid computer.
- 3. Contribution in kind by our collaborators at *Bernstein Center for Computational Neuroscience* (Renato Duarte) and Computational and Systems Neuroscience at *Forschungszentrum Jülich* (Abigail Morrison).
- 4. Two years of BQ1N PhD will be funded by MPI.

BQ1N Research plan

PhD	Year 1	Year 2	Year 3	Year 4
Develop basic network model of mental lexicon	Х	Х		
Addition of mechanisms of long-term plasticity		Х	Х	
Investigation of consolidation in acquisition			Х	Х
Development of tools for network analysis and visualization	Х	Х	Х	
Application to spoken word recognition				Х

Postdoc	Year 1	Year 2	Year 3	Year 4
Supervision and guidance of PhD project	Х	Х	Х	Х
Further development of unification model	Х	Х	Х	
Integration of mental lexicon model into combined architecture		Х	Х	Х
Study interactive effects of unification on retrieval and vice versa			Х	Х
Application to semantic parsing of naturalistic corpora				Х

Linking computational models to neurobehavioral data

To test whether our models can explain human linguistic processing, we will validate them against neural and behavioral data. Recent work by members of the BQ1 team has shown that neural data from such studies can successfully be linked to high-level predictions from computational language models (Frank et al., 2015; Willems et al., 2016). From the point of view of encoding, the question is whether we can predict neural ad behavioral responses to rich and dynamically changing linguistic input. An ability to do so informs about which brain regions are sensitive to what kind of linguistic input as well as

which moments in time different kinds of linguistic input are processed. Conversely, from the point of view of decoding, the question is whether we can reconstruct linguistic input from neural activity patterns. The reconstructed linguistic input will inform about to what extent our computational models are able to capture the full richness of natural language encoded in neural activity patterns.

The goal of this work package (**BQ1D**) is to advance the state of the art in both encoding and decoding of linguistic representations. To this end, we build on and significantly expand on research in this area that has been conducted in the Donders Centre for Cognition. We propose to develop a modeling framework that allows seamless testing of new linguistic models against neural data. In the following, we outline this computational framework as well as the fundamental objectives that need to be addressed.

The to-be-developed framework should be flexible enough such as to accept any linguistic model as its input and any form of neural data as its output. To this end, we propose to use recurrent neural networks (RNNs). In our ongoing work, we have found that RNNs that make use of long-short term memory units allow predicting how sensory stimuli induce (delayed) neural responses (Güçlü & van Gerven, 2016). The goal of this project is to further develop this machinery in the context of Lil. This requires a number of theoretical and technological advances.

First, there is a need to invest in <u>improving the efficiency</u> of the available RNN algorithms to allow testing of potentially very large computational linguistic models against neural data. This can be achieved by incorporating new algorithmic advances, by further optimization of the existing algorithms and by providing the infrastructure to run models on GPUs and on cloud services.

Second, the development of <u>more powerful RNN models</u> such as deep RNNs, bidirectional RNNs, neural Turing machines, or other means to endow RNNs with memory will expand the scope and thereby the usability of the framework. These extensions will be provided by this project. To maximize sensitivity, the framework will also need to be equipped to deal with physiological and other confounds and be able to combine data from multiple subjects, e.g. via hyper-alignment (Haxby et al., 2011). The dynamics inherent to RNNs also provides an avenue to go beyond single words and capture neural correlates of text processing. We plan to use the developed RNNs in this context.

Third, in order to ensure <u>interpretability</u> of the models, we will provide visualizations of the internal states of the RNN as well as their mapping to brain areas (e.g. by linking to FreeSurfer and pyCortex).

Fourth, we will develop a statistical framework which facilitates comparison of alternative computational models. We envision that researchers will be able to provide computational models and neural data based on which the framework automates model comparison. Also, we will provide the functionality to simulate how brains respond to new linguistic input.

Finally, we propose to develop techniques that allow for the <u>decoding</u> of linguistic information from brain measurements. Such a decoding approach has been successfully used by BQ1 team members in prior work in the visual domain (Güclü & Van Gerven, 2015; Schoenmakers et al., 2013). Here, we aim to make the approach suitable for the reconstruction of linguistic information (Pasley et al., 2012) based on RNNs.

The result of this project will be a general framework which allows easy testing of arbitrary computational models against neural data. The framework will be written in Python and made freely available to the community. To achieve our goals, various new techniques need to be developed and implemented. Furthermore, an investment must be made to arrive at a framework which can be used by the community as a whole. To this end, we ask for one 4-year postdoc who will continually develop and improve the framework throughout the course of this project. The Donders Centre for Cognition will provide the infrastructure and computational resources to facilitate the development of the described modeling framework.

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BQ1D research plan

	Year 1		Year 2	Year 3	Yea	r 4
Developing the initial framework to allow computational models						
to be coupled to neural data (initial code base, website for dissemination)	Х					
Improving efficiency of the framework (algorithm optimization, GPU computing); development of statistical framework for model comparison		x				
Developing advanced extensions; improving model sensitivity			Х	Х		
Developing decoding techniques					Х	
Implementation of visualization techniques; dissemination of final framework						Х
Add documentation, optimize code and implement features proposed by LII members	2	×	Х	Х	×	Ĺ

As mentioned before, in addition to the development of more sophisticated analysis techniques, it is important to realize that our modeling efforts critically depend on the availability of suitable data. Language in Interaction offers a unique possibility to collect the large amount of linguistic data that is needed to make this project a success. Such an endeavor requires a tight collaboration between stakeholders in the different BQs (in particular, 2 and 4) as BQ 1 focuses on model development and evaluation rather than data collection. Initially, the project can also make use of existing neuroimaging datasets that have been acquired by our own groups (e.g. in the <u>MOUS</u> and BIG-L projects). Of particular interest are data sets that were acquired while participants were processing rich linguistic stimuli over extended periods of time. Such data sets are available from a local project on narrative comprehension, as well as by external parties (e.g. <u>studyforrest.org</u>).

Overall project management

Big Question 1 will be led by a steering group formed by the first supervisors of the four subprojects, which includes the project coordinator: Zuidema, Frank, Petersson and Van Gerven. All team members commit to frequently attending the planned bimonthly meetings where PhD-students, postdocs and other team members report on progress and update each other on developments in their subfields.

Feedback from Scientific Advisory Board

In response to the previous version of the proposal, the SAB suggested to (1) reduce the number of research questions, (2) increase the linguistic sophistication, (3) recruit additional linguistic expertise, and (4) elaborate on the potential leverage of BQ1. We incorporated these suggestions as follows:

- In the original proposal, the current subproject BQ1P was divided into two subprojects, one focusing on the perceptual properties of words and the second on including information about nonlinguistic modalities. The scope of the second subproject has been greatly reduced, allowing merging of the two subprojects. Also BQ1N was divided into two subprojects, with one focused on processing and the other on acquisition. The acquisition-aspect has been deemphasized, also allowing merging of these two subprojects.
- 2. The description of subproject BQ1L now goes into much more detail on the linguistic issues that motivate the proposed research. Although the focus remains on computational modeling, the linguistic ambitions are now clearly spelled out, with a division of labor between the postdoc position and the PhD position, where in the latter the range of linguistic phenomena that motivate specific linguistic formalisms are now spelled out.
- 3. The supervisory team for both positions in BQ1L now includes Dr Jakub Szymanik, a specialist in compositional semantics (in particular quantifier theory). The research team for BQ1L at large will also include specialists in lexical semantics and cognitive linguistics. The supervisory team for BQ1P now includes Prof. Mirjam Ernestus, a specialist in speech comprehension,

psycholinguistics and the mental lexicon. The research team for BQ1L at large will also include phonologists, computational linguists and psycholinguists.

4. By involving a great number of ongoing PhD-projects and other research projects under the umbrella of BQ1, we aim to have a much bigger impact on the field than could be realized with the 6 requested positions on their own. Moreover, we have made more explicit how BQ1 can inform and support the other Big Questions.

Links to other BQs

We see several links to the other Big Questions, in particular BQ2 and BQ4:

- The developed models will be evaluated against neuroimaging data that is collected in BQ2 and BQ4;
- The role of prior structure in BQ1N's neural processing models can be informative to research in BQ2;
- Individual differences can be captured by variance in the orthographic/phonological, morphosyntactic, and semantic vector representations developed in BQ1L and BQ1P (e.g. due to difference in training data or parameter setting), which may be able to account for findings from BQ4;
- At a technical level, some of the modelling proposed in BQ3 can benefit from the extensive modelling expertise that exists and will further be developed in BQ1.

References

Altmann, G.T.M. & Kamide, Y. (1999). Incremental interpretation at verbs: Restricting the domain of subsequent reference. *Cognition* 73, 247–264.

Baroni, M. & Zamparelli, R. (2010). Nouns are vectors, adjectives are matrices: Representing adjective-noun constructions in semantic space. *Proceedings of the 2010 Conference on Empirical Methods in Natural Language Processing*. Association for Computational Linguistics.

Bowman, S. R., Potts, C., & Manning, C.D. (2015). Recursive neural networks can learn logical semantics. ACL-IJCNLP 2015. Buonomano, D. V. & Maass, W. (2009). State-dependent computations: Spatiotemporal processing in cortical networks. Nature Reviews Neuroscience 10, 113–125.

- Brette, R. & Gerstner, W. (2005). Adaptive exponential integrate-and-fire model as an effective description of neuronal activity. *Journal of Neurophysiology 94*, 3637–42.
- Chen, J.-Y., Lonjers, P., Lee, C., Chistiakova, M., Volgushev, M., & Bazhenov, M. (2013). Heterosynaptic plasticity prevents runaway synaptic dynamics. *Journal of Neuroscience* 33, 15915–15929.
- Clopath, C., Ziegler, L., Vasilaki, E., Büsing, L., & Gerstner, W. (2008). Tag-trigger-consolidation: A model of early and late long-term-potentiation and depression. *PLoS Computational Biology 4*, e1000248.
- Coecke, B. Grefenstette, E. & Sadrzadeh, M. (2013). Lambek vs. Lambek: Functorial vector space semantics and string diagrams for Lambek calculus. Annals of Pure and Applied Logic 164.11: 1079-1100.

Davis, C. J. (2010). The spatial coding model of visual word identification. Psychological Review, 117, 713-758.

- de-Wit, L., Alexander, D., Ekroll, V., & Wagemans, J. (2016). Is neuroimaging measuring information in the brain? *Psychonomic Bulletin & Review*, 1–14.
- Duarte, R. C. F. & Morrison, A. (2014). Dynamic stability of sequential stimulus representations in adapting neuronal networks. Frontiers in Computational Neuroscience 8, 1–20.
- Elman, J. L. (2004). An alternative view of the mental lexicon. Trends in Cognitive Sciences 8, 301–306.
- Fillmore, C., Ruppenhofer, J., & Baker, C. (2004). Framenet and representing the link between semantic and syntactic relations. In: Huang, C. & Lenders, W. (Eds.), *Frontiers in Linguistics*, Academia Sinica, Taipei, pp. 19–59.
- Frank, S. L., Otten, L. J., Galli, G., & Vigliocco, G. (2015). The ERP response to the amount of information conveyed by words in sentences. *Brain and Language, 140*, 1-11.
- Fitz, H., Hagoort, P., & Petersson, K. M. (2015). Sentence comprehension spiked. Presented at Architectures and Mechanisms for Language Processing, Valletta, September 3–5.
- Fitz, H., Uhlmann, M., van den Broek, D., Duarte, R., Hagoort, P., & Petersson, K. M. (2016). Silent memory for language: Insights from neurobiological modelling. Manuscript in preparation.

Frey, U. & Morris, R. G. M. (1997). Synaptic tagging and long-term potentiation. *Nature* 385, 533–536.

Gallistel, R. C. & King, A. P. (2010). Memory and the Computational Brain. Wiley-Blackwell.

Gerstner, W., Kistler, W. M., Naud, R., & Paninski, L. (2014). Neuronal Dynamics: From Single Neurons to Networks and Models of Cognition. Cambridge, UK: Cambridge University Press.

Goldberg, A. (2006). Constructions at Work: The Nature of Generalization in Language. Oxford University Press.

- Güçlü, U., & van Gerven, M. A. J. (2015). Deep neural networks reveal a gradient in the complexity of neural representations across the ventral stream. *The Journal of Neuroscience*, *35*(27), 10005–10014.
- Güçlü, U., van Gerven, M.A.J., 2016. Modeling the dynamics of human brain activity with recurrent neural networks. Frontiers in Computational Neuroscience. Submitted.
- Hagoort, P. (2005). On Broca, brain, and binding: A new framework. Trends in Cognitive Sciences 9, 416-423.

Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. Frontiers in Psychology 4, 1–13.

Hannagan, T., Magnuson, J., & Grainger, J. (2013). Spoken word recognition without a TRACE. Frontiers in Language Sciences, 4, 563.

Hasson, U., Chen, J., & Honey, C. J. (2015). Hierarchical process memory: Memory as an integral component of information processing. *Trends in Cognitive Sciences* 19, 304–313.

Haxby, J. V, Guntupalli, J. S., Connolly, A. C., Halchenko, Y. O., Conroy, B. R., Gobbini, M. I., ... Ramadge, P. J. (2011). A common, high-dimensional model of the representational space in human ventral temporal cortex. *Neuron*, 72(2), 404–416.

Hopfield, J. J. & Brody, C. D. (2000). What is a moment? "Cortical" sensory integration over a brief interval. *Proceedings of the National Academy of Sciences* 97, 13919–13924.

Izhikevich, E. M. & Edelman, G. M. (2008). Large-scale model of mammalian thalamocortical systems. *Proceedings of the National Academy of Sciences 105*, 3593–3598.

Jackendoff, R. (2002). Foundations of Language: Brain, Meaning, Grammar, Evolution. Oxford: Oxford University Press.

Jackendoff, R. (2007). A Parallel Architecture perspective on language processing. Brain Research 1146, 2–22.

Kay, K. N., Naselaris, T., Prenger, R. J., & Gallant, J. L. (2008). Identifying natural images from human brain activity. *Nature*, 452, 352–355.

Kanerva, P. (2009). Hyperdimensional computing: An introduction to computing in distributed representation with highdimensional random vectors. *Cognitive Computation* 1.2, 139-159.

Le, P. and Zuidema, W. (2015). The Forest Convolutional Network: compositional distributional semantics with a neural chart and without binarization. Proceedings of the 2015 Conference on Empirical Methods in Natural Language Processing. Association for Computational Linguistics.

Levelt, W. J. M. (1989). Speaking: From Intention to Articulation. Cambridge, MA: MIT Press.

Lisman, J. E. (1985). A mechanism for memory storage insensitive to molecular turnover: A bistable autophosphorylating kinase. *Proceedings of the National Academy of Sciences 82*, 3055–3057.

Maass, W., Natschläger, T., & Markram, H. (2002). Real-time computing without stable states: A new framework for neural computation based on perturbations. *Neural Computation* 14, 2531–2560.

Markram, H., Wang, Y., & Tsodyks, M. (1998). Differential signaling via the same axon of neocortical pyramidal neurons. Proceedings of the National Academy of Sciences 95, 5323–5328.

Mitchell, T., Shinkareva, S. V., Carlson, A., Chang, K., Malave, V. L., Mason, R. A., & Just, M. A. (2008). Predicting human brain activity associated with the meanings of nouns. *Science*, *320*, 1191-1195.

Monaghan, P., Shillcock, R.C., Christiansen, M.H., & Kirby, S. (2014). How arbitrary is language? *Philosophical Transactions* of the Royal Society B, 369: 20130299.

Mongillo, G., Barak, O., & Tsodyks, M. (2008). Synaptic theory of working memory. Science 319, 1543–1546.

Nieuwland, M. S. & van Berkum, J. J. A. (2006). When peanuts fall in love: N400 evidence for the power of discourse. *Journal* of Cognitive Neuroscience 18, 1098–1111.

O'Donnell., T.J. (2015), Productivity and Reuse in Language: A Theory of Linguistic Computation and Storage.MIT Press.

Palmer, M., Gildea, D., & Kingsbury, P. (2005). The Proposition Bank: An annotated corpus of semantic roles. *Computational Linguistics 31*, 71–105.

Pasley, B. N., David, S. V, Mesgarani, N., Flinker, A., Shamma, S. A., Crone, N. E., ... Chang, E. F. (2012). Reconstructing Speech from Human Auditory Cortex. PLoS Biology, 10(1), e1001251.

Petersson, K. M. (2008). On Cognition, Structured Sequence Processing and Adaptive Dynamical Systems. *Mathematical and Statistical Physics Subseries, Proceedings of the American Institute of Physics 1060*, 195-200. http://dx.doi.org/10.1063/1.3037051.

Petersson, K. M. & Hagoort, P. (2012). The Neurobiology of Syntax: Beyond String-Sets. *Philosophical Transactions of the Royal Society B* 367, 1971–1883.

Pfister, J.-P. & Gerstner, W. (2006). Triplets of spikes in a model of spike timing-dependent plasticity. *Journal of Neuroscience* 26, 9673–9682.

Rabinovich, M., Huerta, R., & Laurent, G. (2008). Transient dynamics for neural processing. Science 321, 48-50.

Rigotti, M., Barak, O., Warden, M., Wang, X.-J., Daw, N., Miller, E., & Fusi, S. (2013). The importance of mixed selectivity in complex cognitive tasks. *Nature 497*, 585–590.

Schoenmakers, S., Barth, M., Heskes, T., & van Gerven, M. A. J. (2013). Linear reconstruction of perceived images from human brain activity. *NeuroImage*, *83*, 951–961.

Socher, R., Perelygin, A., Wu, J. Y., Chuang, J., Manning, C. D., Ng, A. Y., & Potts, C. (2013,). Recursive deep models for semantic compositionality over a sentiment treebank. In *Proceedings of the Conference on Empirical Methods in Natural Language Processing (EMNLP)* (Vol. 1631, p. 1642).

Song, S., Miller, K., & Abbott, L. (2000). Competitive Hebbian learning through spike-time-dependent synaptic plasticity. *Nature Neuroscience* 3, 919-926.

Steedman, M. (2000). The syntactic process. Cambridge: MIT Press.

Stokes, M. G. (2015). 'Activity-silent' working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences 19*, 394–405.

Turrigiano, G. G. (2012). Homeostatic synaptic plasticity: local and global mechanisms for stabilizing neuronal function. *Cold Spring Harbor Perspectives in Biology 4*, a005736.

van Cranenburgh, A., & Bod, R. (2013). Discontinuous parsing with an efficient and accurate DOP model. In *Proceedings of the International Conference on Parsing Technologies (IWPT 2013)*.

Vogels, T. P., Sprekeler, H., Zenke, F., Clopath, C., & Gerstner, W. (2011). Inhibitory plasticity balances excitation and inhibition in sensory pathways and memory networks. *Science* 334, 1569–1573.

Willems, R. M., Frank, S. L., Nijhof, A. D., Hagoort, P., & Van den Bosch, A. (2016). Prediction during natural language comprehension. *Cerebral Cortex 26*, 2506-2516.

Wills, S. A. (2004). Computation with Spiking Neurons. PhD thesis, University of Cambridge, UK.

Zenke, F., Agnes, E. J., & Gerstner, W. (2015). Diverse synaptic plasticity mechanisms orchestrated to form and retrieve memories in spiking neural networks. *Nature Communications 6*, 1–13.

7. Knowledge utilization

If a theory is embodied successfully in a computational model it is likely that, next to carrying scientific insight, the algorithm can be reused and potentially put to practical use. The developed software, simulation environment, and models will be made publically available for the scientific community and the public at large. Applications of the computational methods developed in this proposed project can assist the general use, understanding and acquisition of language by a broad user base, and will in the longer run have the potential to increase societal equality and raise the quality of life for patients.

Our main utilization aims are:

- To provide support for making the collected data available to the research community;
- To release the software underlying all developed computational models as open source software that can be used by the research community, and/or as web-services and free apps for the end user.

In particular, we foresee (and intend to stimulate) knowledge utilization in the following areas:

- Assistive technology for communication support. Computational language models are the natural basis for personalized, accurate text completion and correction algorithms that can facilitate text entry for people with communicative challenges (e.g. paralysis, aphasia) and for low-literate persons. The same technologies could become staple technologies in generic text entry systems ranging from word processors to mobile devices.
- Enhanced learning of first and second languages. Insights into representing, using, and acquiring a mental lexicon, in first-language but also second-language learning contexts, could find a translation into enhanced methods for aspects of language learning, such as vocabulary training and cross-modal language learning.
- **Brain-computer interfaces**. Applications for 'thinking aloud through machines' could emerge from the model evaluation component of this proposal, opening up vast possibilities for improving patient care and quality of life of patients, but also potentially broader communicative and learning goals.
- **Dissemination**. The standard channels for scientific communication will be used, including presentations at scientific conferences and research publications. We also intend to organize workshops (e.g. at the Lorentz Center) with leading experts on the mental lexicon and the various aspects outlined in this proposal, including vector representations of lexical items, computational neuroscience, and machine learning approaches to large datasets.

We will pick the examples to elaborate on pragmatic grounds, optimizing impact and taking care that indeed a broad spectrum of utilization is addressed. For the development of apps we follow the <u>approach</u> already developed by the Knowledge Utilization work package (WP7) of the Language in Interaction Consortium.

8. Research data management

We intend to make use of data collected in other projects. Software maintenance during the project lifetime will be supported by proper distributed versioning systems (e.g. github), backup, and marking releases with the proper persistent identification (e.g. DOIs through Zenodo). After the project lifetime measurements will be taken (to be specified in a Data Management Plan established at the start of the project) to preserve data and software created within the project; the storage and archiving facilities of DANS (EASY) would currently be the most apt solution.

BIG QUESTION 2

1. Big Question coordinator: Prof.dr. Peter Hagoort

2. Title of the Big Question

What are the characteristics and consequences of the internal brain organization for language?

3. Key words

language connectomics, language related gene activity, oscillatory activity, subcortical structure, predictive architecture, language universals

4. Scientific summary of research proposal

The human brain provides a neurobiological infrastructure that allows us to acquire and process language, and that co-determines the characteristics of spoken (and sign) and written language. The internal organization of the brain and its cognitive architecture both determine and constrain the space of possibilities for human language. This internal organization can be called the Kantian brain for language. It has resulted in a language-readiness of the human brain that is found nowhere else in the animal kingdom. The big question is to characterize the Kantian brain for language. This question has two sides: (i) what is the internal brain organization that supports language? (ii) in what way did speech and language adapt their characteristics to the intrinsic organization of the human brain (the quest for language universals)? In this proposal we will mainly focus on the internal brain organization for language (i.e. aspect (i) of the overarching question).

5. Composition of the project group

Name and title	Specialisation	Institution	Lil Work Package	Involvement
Peter Hagoort	Neurobiology of Language	DCCN & MPI	3	Coordinator
Simon Fisher	Molecular Genetics of Language	MPI	5	genetic aspects of language
Roy Kessels	Clinical Neuropsychology	DCC	6	application in clinical environment
David Norris	MR Physics applied to Cognitive Neuroscience	DCCN	6	MRI technique
Ardi Roelofs	Language & attention	DCC	4	cognitive neuroscience of language and cognitive control
Elia Formisano	Neural basis of human auditory perception and cognition	Maastricht University	1	neuroimaging research on the auditory/speech perception system.
Antje Meyer	Experimental psycholinguistics	MPI	5	knowledge of experimental psycholinguistics

List of consortium members of the project group

Nick Ramsey	Human Brain imaging, valorisation	Utrecht University Medical Center	6&7	expertise in imaging technologies and valorisation
Christian Beckmann	Computational methods for data understanding and neuroimaging	DCCN	6	methods for image analysis, machine learning and imaging statistics
Karl-Magnus Petersson	Neurobiology of language processing, reading & writing, and learning & memory	MPI	3	neurobiologically realistic computational models of language processing
Ivan Toni	Motor cognition	DCCN	1	neural and cognitive mechanisms that turn a thought into a movement,
Hans Rutger Bosker	Psychological mechanisms in speech production and perception	MPI	5	speech
Vitoria Piai	Neurological disorders in language, control & and memory	DCC/DCN		neurological disorders in a clinical setting

List of non-consortium members of the project group

Name and title	Specialisation	Institution	Involvement
Anne Kösem	Neurobiology of speech	MPI	role of brain oscillations for speech processing
Julia Udden	Neurobiology of language	MPI	bridging to ongoing work (e.g. the MOUS project) investigating questions related to those of the current proposal. Uses neuroimaging (FMRI, DWI) and genetics to study sentence processing.
Alexis Hervais-Adelman	Neurobiology of Language	MPI	neuroscience of simultaneous interpretation, relationship between executive functions and multilingual control, mechanisms of degraded speech comprehension.
Floris de Lange	Perception, cognition, and behavior	DCCN	neuroimaging research on prediction research in perception and language
Rogier Mars	Organisation of primate brain	DCC& Univ. Oxford	acquisition and analysis of comparative primate neuroanatomy data, developing and applying methods for linking brain architecture to function, and providing evolutionary perspective on brain networks for language
Clyde Francks	Genetic basis of brain asymmetry and its links to variation in human cognition	MPI	language-related gene activity
Tineke Snijders	(Individual differences in) language processing in the brain (infant, adult)	DCCN	neural dynamics speech and language comprehension, oscillations, developmental aspects, individual differences

Jan Mathijs Schoffelen	Interaction between	DCCN	optimization of MEG data acquisition and
	brain regions		analysis, implementation and optimal
	(connectivity		application of advanced analysis tools.
			MEG data workflow management.
Sara Aurtenetxe	MEG, oscillations,	DCCN	expertise on mild cognitive impairment
	language, aging		and aging effects

6. Description of the proposed research within the Big Question

(I) The internal brain organization for language

The internal brain organization that supports language should be studies at multiple levels, at the neuroanatomical level (in a cross-species comparative way), at the neurophysiological level, and at the functional level. The neuroanatomical level includes the connectivity profile of the human brain. Cross-species comparisons using DTI and resting state measurements might provide insights into the crucial features of the connectome for language. What are the unique features of the human connectome in comparison with other species that might have enabled us to have a richer system for communication than can be found anywhere else in the natural world? It also includes the cyto-, myelo-, and receptorarchitectonic properties of perisylvian areas that might have contributed to the neurobiological infrastructure of the language-ready brain. In this research effort we will, however, focus especially on the language connectome. In recent years, advances in neuroimaging have given unprecedented access to in vivo measurements of brain function, structure and connectivity. Moving away from simple models of local processing, the field is increasingly shifting towards characterising the interactions between distributed functional brain networks and associated white-matter structures that support these networks. Accordingly, application of FMRI in cognitive neuroscience has shifted from associating effect size differences in isolated regions of the brain to relating cognitive function to communication and functional integration among large-scale functional brain networks of correlated activity (e.g., 'Resting-State Networks', RSNs) and supporting axon fiber infrastructure. Such Connectivity data can be used to investigate boundaries between functional regions, based on the assumption that areas with different connections have different functional characteristics. However, the relationship between connectivity and areal boundaries is complex, and no consensus exists on the most reliable, robust and functionally relevant method for connectivity-based parcellation (e.g. boundaries are not always "sharp", as cell populations mix across certain borders). The spatial and temporal information available from structural, diffusion and functional MRI and MEG, are highly complementary to each other, and together form a collection of modalities that offer massive potential for simultaneous modelling of the tissues, structures and functional networks in the brain. We will utilise measures of functional and structural connectivity to shed lights on the underlying building blocks that support the features for the connectome of language. Abstracting from specific language tasks we will use the connectomic description at the systems neuroscience level to enable crossspecies comparisons in order to characterise the unique features that enable human connectivity over and beyond levels of communication found in other species. We will look at the temporal-frontal tracts across a wider range of species post mortem, including humans, apes (chimpanzee, gorilla), and monkeys (macaque, baboon) to test which innovations occurred where on the evolutionary tree. We will also collect data on local anatomy, such as myelin maps, so that we can determine not just the course of tracts, but also the nature of their target areas. This is essential given the observation that large parts of temporal cortex have been reorganized since the last human/non-human common ancestor. We will also investigate the underlying laminar structure of both regions that activate in specific language tasks, and those defined by the termination of important anatomical pathways (e.g., arcuate fasciculus), to explore whether these regions have a homogeneous morphology; thus

elucidating structure/function relationships at a fine spatial scale. Moreover, whereas a lot has been learned through functional neuroimaging on what is "special" about processing of speech in the human brain, much less is known on how speech influences neural processing mechanisms on the level of the (acoustic) features that speech has in common with other natural sounds. It is conceivable that in the course of human evolution "general purpose" (cortical and subcortical) mechanisms of sound analysis have become optimized for speech processing. As the influence of speech on general-purpose brain processing mechanisms is uniquely expected in humans, performing model-based experiments and analyses in non-human species (e.g., with fMRI in non-human primates) adds a crucial evolutionary perspective to testing these hypotheses and to interpreting the results of experiments in humans.

Language related gene activity

A related challenge is to characterize the molecular genetic infrastructure that supports the languageready brain. It remains poorly understood what combinations of genes and proteins (receptors, ion channels etc.) distinguish cortical and other regions of the language system in the brain. The molecular profiles of these regions are likely to tune their electrophysiological and other functional properties to influence aspects of both connectivity and oscillations. Transcriptomic analysis of postmortem human brain allows mapping of gene expression profiles (mRNA) within cortical and subcortical excisions from defined neuroanatomical regions. Transcriptomic analysis generates a quantitative profile of gene expression values across most of the thousands of active genes within a given tissue section, including for example genes involved in ion conductance and synaptic transmission. Publicly available datasets have been generated from small numbers of brains using an older technology for expression analysis (micro-arrays), and without focusing specifically on languagerelated regions. Gene expression profiles of anatomically distinct regions of the cerebral cortex have been shown to correlate, when those regions are parts of defined resting-state connectivity networks. Thus transcriptomic profiles may be interpreted to as genetic markers of network connectivity, and have the potential to enhance the precision of connectivity models. However, language-related networks have not been studied in this regard. There is clear potential to improve the state-of-the-art in relation to language, by focusing on core brain regions and networks involved in language, and applying the latest technology for RNA sequencing, which offers improved sensitivity and accuracy. Possible sources of post mortem brain tissue include the Netherlands Brain Bank. We therefore propose to carry out an improved mapping of the brain's infrastructure for language at the level of gene activity, using RNA sequencing and transcriptome profile analysis. Cortical regions involved in language networks' resting and active states will be targeted, as well as 'control' regions outside of language networks, as defined by leading experts in our Lil consortium. Existing and publicly available data will be integrated into the project where applicable. We are also setting up a collaboration with leading experts from Juelich, for mapping functionally defined regions to post mortem anatomy. Note that this analysis, necessarily based on relatively small numbers of human brains, is targeted at describing the genetic setup of a 'typical' human brain. This may also relate to data on neurotransmitter receptor mapping in the post mortem human brain that is carried out by the researchers from Juelich. Genetic profiles that are characteristic of language-related networks will be further investigated in a comparative context, with a view to defining whether the driver genes (those whose activity is most correlated with language network membership) show genomic evidence for relatively increased evolutionary changes compared to apes, thus approaching the uniqueness of the brain's architecture for language.

Oscillatory contributions

Another important architectural feature relates to the neurophysiological infrastructure. One central question relates to the role of brain oscillations (e.g., delta, theta, gamma) as a mechanism of parsing

the speech input in multiple temporal units that map onto the relevant informational units of speech (phrases, syllables, phonemic segments). At the same time, oscillations in different frequency bands play a role in higher order language processes (such as syntactic and semantic unification). How one can envision these intrinsic oscillation to play a mechanistic role in different aspects of speech and language processing, as well as in multimodal aspects of language processing, is still largely unexplored.

One way in which the intrinsic brain organization shapes language, and speech in particular, relates to the role of brain oscillations in speech perception. Neural oscillations have been proposed to parse the speech signal into temporal units that map onto corresponding informational units of speech, thus shaping speech comprehension. However, a comprehensive understanding of the interplay between neural oscillations and language processing is lacking. Firstly, it remains unclear whether (and how) the phase-locking of different neural oscillations to the speech signal causally influences the perception of that signal, or whether the oscillations merely follow the amplitude fluctuations of the speech input. Current speech models are in support of the first view, and predict that manipulations in brain oscillatory activity should modify speech processing and ultimately constrain perception. Ways in which neural oscillatory activity in auditory cortices could be modulated experimentally are, for instance, manipulating a preceding rhythmic sensory input (e.g., speech rate), or potentially by means of transcranial alternating current stimulation (tACS). Studies on covert speech also provide additional promising experimental methods to tease apart endogenous from stimulus-driven brain-speech tracking mechanisms.

Second, the specific roles of neural oscillations for higher order language processes need still to be evaluated. Strong modulations of neuronal oscillations are observed in language comprehension tasks. Examples are modulations of oscillations in the theta, alpha, beta and gamma band in various perceptual and language areas. Recently, studies have investigated the cross-frequency interactions between these oscillations in relation to various cognitive tasks. As demonstrated by animal research, these oscillations are involved in the temporal coordination of neuronal coding and have been suggested to be involved in establishing task-dependent functional connectivity between regions. For instance phase-synchronization of oscillations in lower frequency bands (e.g., theta and alpha bands) seems to reflect top-down controlled exchange of information between regions. The actual feedforward exchange of information is reflected by gamma band synchronization. We will use this insight to interpret findings on oscillations in a set of language experiments in which anticipatory prediction and integration are manipulated. Further, we will relate structural to functional connectivity. As an example, the arcuate fasciculus connects lateral frontal to temporal regions and can be identified using DTI. We will ask if hemispheric lateral asymmetries in the left versus right fasciculus are predictive of hemispheric asymmetries in the modulation of oscillations during language comprehension tasks. In addition, based on earlier work, we will relate the oscillatory responses to the BOLD effects in fMRI, contributing to a deeper insight in the spatial distribution of the oscillatory effects. This will be achieved by using simultaneous EEG/fMRI, which we will use as a tool to explore the degree to which the phase of given EEG oscillations is predictive of the BOLD response. This will make it possible to relate oscillatory signals to the underlying anatomical substrates and offer an indirect mechanism for exploring signal changes in regions where MEG/EEG source modelling may fail, for example the subcortical structures (see below).

As an overarching goal we will seek to integrate the oscillatory frameworks for speech perception and language comprehension. While these perspectives have been developed in parallel, they share several components such as prediction and context dependent routing of information between regions. Part of this endeavor will be to use multimodal approaches combining speech, reading, and sign language studies to disentangle sensory and language-specific neural oscillatory mechanisms.

The role of subcortical structures

Understanding the internal brain organization for language not only requires studying cortical structure and function, as has traditionally been done and still is typically done, but also requires the investigation of subcortical structures, such as the basal ganglia and the thalamus. These structures are widely connected to the neocortex, yielding the basal ganglia thalamocortical circuitry (BGTCC). This circuitry is present in all vertebrates. Its importance for language is suggested by the implication of the BGTCC in sound production learning (i.e., song in vocal learning birds, speech in humans), whereas the circuitry is not implicated in the vocal behavior of non-learning animals (i.e., vocal nonlearning birds and nonhuman primates). In line with this finding, developmental language impairment in humans is associated with anomalies of the BGTCC. Persons with Parkinson's disease, which impairs the functioning of the BGTCC, show language production deficits. Moreover, focal BGTCC damage in adult stroke patients often yields a range of language impairments, including speech initiation difficulty, lexical processing problems, and agrammatism. Also, the involvement of the circuitry is suggested by hemodynamic neuroimaging studies of adult language performance. However, little is known about exactly what the contribution of the BGTCC to language is. The BGTCC consists of a number of parallel loops, including a cognitive loop involving the caudate and a motor loop involving the putamen. Do these loops underpin different aspects of language production (e.g., is the caudate implicated in lexical selection and the putamen in phonological/phonetic encoding)? Moreover, it has been suggested that the BGTCC is important for training cortical connections and that frontal cortical regions are responsible for automatic processes after extensive training. Does this also hold for language (e.g., is the BGTCC implicated in the production of novel phonological forms but not of highly-practiced stored ones)? The proposal is to examine these issues in healthy adult participants using fMRI, and in patients with Parkinson's disease.

Predictive architecture of the brain

A central feature of brain function is assumed to be predictive coding. How does the predictive coding characteristic of functional brain organization map onto the core features of language processing? The human brain capitalizes on the predictable structure of the world, actively anticipating future input to constrain computations. During the unfolding of a sentence, the brain predicts the occurrence of upcoming words, and violations of these predictions result in elevated neural responses. The predictive nature of information processing in the brain might be implemented by predictive coding (PC). This is a neurocomputational model that describes how feedback and feedforward signals within the cortex may embody predictions and the signals to update them (i.e., prediction errors). A central question is how this putative organizational principle of the brain influences or determines the core features of language processing. One essential feature of PC models is the hierarchical organization, in which higher levels in the hierarchy bias the computations of neurons at earlier levels. This has been successfully applied to visual perception, explaining several context effects. It is plausible that similar operations are at work in language, in which scene parsing could be likened to parsing a paragraph, while object recognition can be viewed as parsing a word or sentence. Key questions that are currently outstanding include: (i) How are language operations implemented within the recurrent (hypothesis-testing) neural architecture of the brain? (ii) How do predictions at different levels of the hierarchy (e.g., from low-level sensory and single-word level to sentence and discourse level) conspire to jointly shape the neural response to upcoming linguistic signals? Do predictions at different hierarchical levels have additive predictive effects, or do they influence perception in a hierarchical fashion? These questions will be addressed in a series of combined behavioral and neuroimaging studies in healthy adult volunteers, in which (violations of) linguistic predictions will be manipulated at different hierarchical levels (from low-level sensory predictions afforded by lip placement to semantic and pragmatic information). Outcome measures will be defined at the behavioral level (processing efficiency, reaction times and accuracy), and in terms of electrophysiological predictive and prediction

error signals (anticipatory oscillatory modulations in low frequencies, and post-stimulus, highfrequency activity modulations, respectively). Therefore, the question of the predictive coding architecture has close crosslinks with the question of "oscillatory contributions". Answering these questions will elucidate what the consequences are of a fundamental computational property of the brain – predictive coding – for language processing.

(II) Language universals as a consequence of intrinsic brain organization

The consequences of the Kantian brain for speech and language represents the other side of the Kantian coin. This side focuses on how characteristics of spoken and written language are a reflection of intrinsic brain organization, more specifically on how the overall cognitive architecture of the human mind affects the patterns of cross-linguistic diversity and universal tendencies. For instance, the temporal packaging of informationally relevant units in speech (e.g., segments, syllables) is predicted to be relatively constant across the languages of the world. The different orthographies in writing systems are predicted to show brain-related biases. The preference for certain word orders in the world's languages might reflect cognitive biases in the human information processing architecture. Despite concerted efforts in the field of linguistics to formulate universals that hold across all 6000 languages of the world, the limited success (or failure, depending on one's perspective) could be due to the fact that one has looked at the wrong level of language organization. In this research program, we attempt to derive testable predictions about universal tendencies from a different perpective, namely from the principles of brain organization; principles that are assumed to impose patterns/limitations on the space of possibilities for the core features of speech and language. For instance, if neural oscillations provide general encoding principles for speech processing, this would lead to the (as yet untested) prediction that the temporal characteristics of the world's languages are constrained in their variability due to processing characteristics related the different oscillators. But the complementary observation that there is variation in rhythmic properties between the world's languages can potentially be motivated by neurophysiological variation between populations of speakers. Finally, from an evolutionary perspective, it could also be tested whether languages have developed such that their temporal structure matched the available neural encoding mechanisms. Practically, concrete predictions deriving from neuroanatomical and neurophysiological properties of the human brain can be tested using cross-linguistic samples. For example, predictions concerning the temporal characteristics of syllables and phonemes derived from brain oscillatory mechanisms can be tested by collecting high-quality data from a few judiciously sampled languages or (in a complementary manner) by conducting statistical and phylogenetic analyses on large databases such as the World Phonotactics Database (http://phonotactics.anu.edu.au/index.php) or PHOIBLE (http://phoible.org). Such work would require using relatively well-established methods of data collection and statistical analysis, and will be conducted through collaborations with external partner institutions of the consortium. In the absence of core expertise in the consortium itself, it will not be on the priority to-do list for the coming period.

7. Knowledge utilization

There will be no additional knowledge utilization aspect of this program over and beyond the general knowledge utilization components of the Language in Interaction consortium.

8. Research data management

Research data management will be done according to the RDM procedures and infrastructures of the Donders Institute and the Max Planck Institute.

BIG QUESTION 3

1. Big Question coordinator: Prof.dr. Ivan Toni

2. Title of the Big Question

Creating a shared cognitive space: The use of language in interaction.

3. Key words

conceptual alignment, communicative asymmetries, multimodal interactions, turn-taking, communicative deficits, neurobiology of interaction

4. Scientific summary of research proposal

Language is a key socio-cognitive human function predominantly used in interaction. Yet, linguistics and cognitive neuroscience have largely focused on individuals coding-decoding signals according to their structural dependencies. Understanding the communicative use of language requires shifting the focus of investigation to the mechanisms used by interlocutors to share a conceptual space.

This project will experimentally manipulate and computationally define the complex cognitive space in which interlocutors operate during live communicative interactions. This space is characterized along two constitutive dimensions. First, we consider the temporal structure of communicative interactions, in which an interlocutor can respond to a signal occurring at any time along the interaction's trajectory, irrespective of ordering or syntax. This project tackles these complexities by considering the full temporal range of a dialogue, from rapid switching of turns (sub-second timescale) to mutual adjustment of discourse models (minute timescale). Second, we consider the functional dynamics of real-life communicative interactions. The creation of a shared conceptual space across communicators (alignment) is often intermingled with the interlocutors' exploitation of that space for asserting individual opinions (asymmetry). This project considers the influence of those two dimensions over multiple communicative resources (speech, gestures, gaze) and linguistic structures (from phonology to pragmatics). (Para)linguistic features extracted from structured live interactions of human interlocutors will be used to define the computational architecture, inferential processes, and neurobiological mechanisms implementing the creation and control of a shared cognitive space. We will track how neural markers of individual interlocutors' representations become aligned during the real-life dialogue, which model properties are required to accommodate interlocutors' use of (para)linguistic features, and explain how different linguistic structures are coordinated into a communicative signal.

5. Composition of the project group

Name and title	Specialisation	Institution	Lil-WP	Involvement
Ivan Toni, Prof	Motor cognition, Social neurocognition	Donders Institute	WP1	Research program coordinator
Mirjam Ernestus, Prof	Variation in spontaneous speech	Centre for Language Studies	WP1	Corpus analysis Phonetic alignment
Herbert Schriefers, Prof	Production, comprehension	Donders Institute	WP3	Phonological alignment

List of consortium members of the project group

Asli Ozyurek, Prof	Speech & gesture, Spatial cognition & action	Centre for Language Studies	WP4	Multimodal alignment
Robert van Rooij, Prof	Logical semantics, Pragmatics, Formal modelling	Institute for Logic, Language, and	WP2	Semantic alignment
Christian Doeller, Dr	Spatial representation, fMRI-MVPA	Donders Institute	WP2	Neurobiology of knowledge representation
Harold Bekkering, Prof	Interaction, Prediction	Donders Institute	WP4	Theory of alignment
Stephen Levinson, Prof	Pragmatics of communicative interaction	Max Planck Institute	WP5	Theory of alignment
Pieter Muysken, Prof	Morpho-syntax	Centre for Language Studies	WP5	Syntactic alignment
Pieter Medendorp, Prof	Bayesian modelling	Donders Institute	WP4	Multimodal integration
Jan Buitelaar, Prof	Autism	Donders Institute	WP6	Communicative disorders

List of non-consortium members of the project group

Name and title	Specialisation	Institution	Involvement
Mark Blokpoel, Dr	Computational cognitive modelling	CiTec	Theory of alignment
Raquel Fernandez, Dr	Computational dialogue modelling	Institute for Logic, Language, and	Asymmetries in dialogue
Mark Dingemanse, Dr	Repair mechanisms in multimodal interaction	Max Planck Institute	Dialogue repair mechanisms
Shiri Lev-Ari, Dr	Cognitive psychology	Max Planck Institute	Social-network effects on alignment
Iris van Rooij, Dr	Computational cognitive modelling	Donders Institute	Theory of alignment
Jakub Szymanik, Dr	Logic, formal semantics, cognitive modelling	Institute for Logic, Language, and	Theory of alignment
Johan Kwisthout, Dr predictive processing theory		Donders Institute	Theory of alignment

6. Description of the proposed research

Overall aim and key objectives

This research program is concerned with the use of linguistic means during interpersonal interactions. The bulk of language use occurs in an interactive setting, namely the context in which it evolved, in which it is learned and which has likely shaped it the most. In a fundamental sense, "Language in Interaction" is about the use of linguistic means for reaching mutual understanding during communicative exchanges. Yet, paradoxically, the study of human communication has rarely been approached in terms of mutual understanding, focusing instead on individual agents producing scripted utterances or processing isolated sentences. For instance, traditional psycholinguistics has largely focused on encoding-decoding of linguistic material as implemented by individual agents, away from the context of interaction with other interlocutors. Generative linguistics has also been largely un-

interested in the actual use of language, claiming that internal structural dependencies cannot be understood by contingent externalizations¹. There are also conceptual and practical difficulties in conducting theoretical and empirical work in a truly interactive setting: It is hard to experimentally control real social interactions, and it is hard to shift theoretical focus from individuals processing signals to interlocutors creating a shared cognitive space.

This research program assumes that the computational problem solved in human communication (in the sense of Marr²) is the creation of a cognitive space shared across communicators^{3–7}. A shared cognitive space involves not only presumed common ground, the propositions jointly taken for granted or communicated, but also mutual awareness of the circumstances of communication, and thus the likely joint goals, norms, and affordances of the event. This perspective considerably broadens the objectives of linguistic enquiry. Besides the traditional focus on transfer of propositional content, this research program considers how language use is organized to predict interaction goals and to monitor mutual understanding. We have the ambition to understand, at the neuronal and at the computational levels, how this shared cognitive space is created and controlled during live communicative interactions, and how different (para)linguistic features of a dialogue are structured within that space. By combining theoretical and empirical investigations, we aim to define how natural language is used to communicate, and how human communication influences language use. This big question is largely left un-answered by existing accounts. Models of alignment in dialogue mostly ignore how language use can be contextually adaptive and computationally realizable, focusing on limiting-case instances like automatic priming of individual experiences with a signal's properties^{8–11}. Crucially, it remains unclear how production and comprehension of an utterance can be concurrently implemented (given that responses must be planned in the middle of turn which is being responded to¹²) and interfaced with the slow updating of mutual understanding occurring during a dialogue^{13–15}. The cognitive and neural mechanisms supporting other integral elements of natural dialogue are also often neglected, e.g. how can interlocutors pursue mixtures of conceptual asymmetries and alignments^{16,17} across different (para)linguistic structures, supporting the disagreements and competitions that are part and parcel of human linguistic interactions.

This research program captures the creation and control of a shared cognitive space during human communication by combining a comprehensive characterization of different features of language use with neurobiological constraints and computational mechanisms. This overall goal is achieved through three key objectives. First, we characterize the production and comprehension of natural linguistic interactions at multiple levels of description (phonology, semantics, gestures) using theoretically-grounded features. Second, we consider how interlocutors coordinate their language use across multiple temporal scales (from milliseconds to minutes) and functional goals (alignment, asymmetry). Third, we provide both computational and neurobiological mechanisms explaining why the communicative use of language is organized in the way it is.

Contribution to the overarching quest of Lil

This project integrates and elaborates on research lines distributed across several Lil work-packages, namely the production and comprehension of spoken language (Lil-WP1), the organization and use of semantic and conceptual knowledge (Lil-WP2), the contextual interpretation of inherently ambiguous signals (Lil-WP3), the contribution of gesture and action to language processing (Lil-WP4), how computational bottlenecks predict individual variation in interactive abilities (Lil-WP5), and pathological alterations in language and communication (Lil-WP6). The structured integration of different research lines will contribute to the overarching quest of Lil by defining the computational and neurobiological constraints that human interlocutors face when using language in interaction. The emphasis is on integration: This project aims at defining how different levels of description and different linguistic features constrain each other during language use, rather than simply juxtaposing each level in isolation without identifying how their interaction is structured.

Scientific relevance and challenges

This research program will make a difference by taking seriously the communicative context in which linguistic signals are used, both empirically and theoretically. We focus on two fundamental features of that context. First, a communicative context is built from phenomena occurring over a broad temporal range, from rapid switches of individual conversational turns to slow alignment of discourse models across interlocutors. Existing empirical approaches have focused on either ends of this range, largely ignoring how interlocutors deal with the interactions between rapid and slow temporal processes occurring during a dialogue. For instance, how is the local predictive processing intrinsic in rapid turntaking coordinated with the multiple long-range dependencies between speech acts observed in multiturn dialogues?⁴ Second, interlocutors often need to shape their language use to accommodate or assert a number of asymmetries in knowledge status. Existing accounts of human communication have often been probed with coordination games, leading to a narrow focus on cooperative aspects. In contrast, natural dialogue often involves asymmetries in the interlocutors' goals, asymmetries that can be accommodated within a shared conceptual space without compromising that space. How does a teacher assert differences in knowledge from her pupil, while striving for her pedagogical goal? During a dialogue, preserving asymmetries at one level (e.g. phonological markers of social status) does not prevent achieving alignment at other linguistic levels, and some asymmetries could even be used to facilitate conceptual alignment. Current models of discourse do not allow for this^{8,10,11,18}.

The scientific challenge of this research program lies in distilling the complexities of interactive language use into theory-driven principles and neurobiological mechanisms. Our approach is to consider the contribution of distinct communicative resources (speech, gestures, gaze) at different levels of linguistic structure (from phonology to pragmatics) during real-life dialogue evoked under both spontaneous and experimentally-controlled situations. For instance, we will index phonological markers (e.g. alignment in vowel quality, intonation patterns, speech rate), syntactic markers (e.g. order of indirect speech acts), and choices of lexical/gestural items (e.g., referring expressions and turn-shifts markers)¹⁹. Those features can then be used to understand how individual communicative signals are disambiguated within the conceptual space defined by the recent history of communicative interactions, both at the formal computational level and the mechanistic neurobiological level. The formal computational understanding is reached building upon existing Game Theoretical and Bayesian models of intention recognition^{20–22}. This level of understanding examines properties of the model that lead to strong computational constraints when considering the (para)linguistic features extracted during the real-life dialogue. The mechanistic neurobiological understanding is reached by tracking how neural markers of individual interlocutors' representations become aligned during the real-life dialogue. This level examines the neural mechanisms that support the dynamics of mutual understanding.

Connections and interdisciplinary collaborations

This is a highly interdisciplinary research program that aims at reaping the benefits of a principled integration across different disciplines. The use of language in interaction is a complex phenomenon that goes well beyond the competence of individual researchers and the boundaries of traditional academic fields. Here we exploit the unique range of expertise mobilized by the Language in Interaction consortium, combining theoretical and empirical approaches across multiple levels of linguistic organization. Expertise from psycholinguistics, conversational analysis, phonology-phonetics, gesture studies, multimodal language analysis, computational linguistics, game theory, Bayesian modelling, computational-level modelling, and cognitive neuroscience is brought to bear on a controlled instance of genuinely interactive social cognition. The rationale is that addressing the same problem at different levels of explanation and using different metrics enriches the explanatory value of each level of analysis with knowledge acquired at the other levels, and generalizes from specific findings to broader principles. The interaction and integration between these different domains of

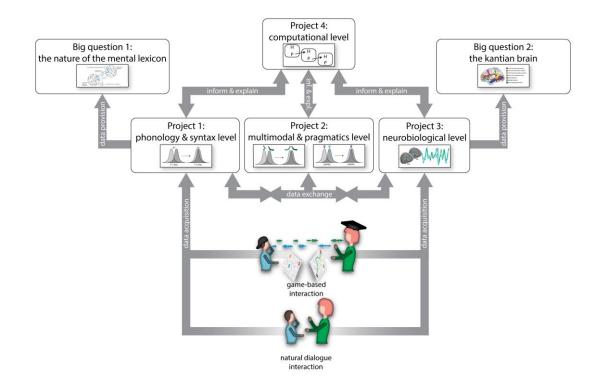


Figure 1. An illustration of the structure and experimental platform of the research program.

expertise is built into the structure of the research program, at multiple levels. For instance, each project is designed to be informed and constrained by the findings from other projects and covers the same temporal window of research (four years). Many senior investigators have expertise and are involved in supervising more than one project, providing an effective mean of aligning knowledge across projects. The team members will also commit to quarterly in-depth meetings (over one/two days) to provide frequent and systematic occasions for integration of the different projects.

Research plan, methods, and techniques

This research program is based on four complementary projects. It is grounded on empirical observations obtained during a) spontaneous dialogue within a naturalistic interaction; and b) structured dialogue within a coordination game (Figure 1). The rationale is to study dialogue within an experimentally tractable platform, and assess the generalizability of those observations against dialogue evoked in a naturalistic setting. The experimentally controlled dialogue is simple enough to be abstracted in computational models and portable to neurophysiological experiments. Yet, it is also flexible enough to capture the complexities of interactive language use addressed in this project. The experimentally controlled dialogue is a well-established visuospatial coordination game involving the negotiation of a path through a map across two interlocutors^{23–25}.

Project #1 will characterize alignment in dialogue at the phonological, syntactic, and semantic level. This project will acquire a comprehensive record of speech, hand/head-gestures, and gaze in pairs of interlocutors engaged in the interactive production and comprehension of utterances evoked during spontaneous dialogue, and during the visuospatial coordination game. Patterns of alignment will be analyzed at different linguistic levels, including phonetics (e.g. alignment in vowel quality, intonation patterns, speech rate), syntax (e.g. how do the speakers realize different indirect speech acts), and semantics (e.g. lexical choice). This approach will make it possible to understand the interaction of

different linguistic levels during alignment, considering both the direction and extent of the alignment and how the alignment develops over time. These findings will provide important empirical constraints for the theoretical work of Project #4 (see below). Furthermore, the corpus data acquired in this project will also be used by Project #2, and made available for the computational analyses on the mental lexicon implemented in the Big Question 1 (Figure 1). We also expect that the corpus-based findings of this project will lead to experimental stimuli (e.g. precisely characterized and representative speech segments occurring during a dialogue) and neural predictions (e.g. timing of neurophysiological events) that can be used for empirical tests in collaboration with Project #3.

This project will be coordinated by Mirjam Ernestus (responsible PI), in collaboration with a supervisory team constituted by Herbert Schriefers (co-promotor for the PhD student), Pieter Muyskens, Mark Dingemanse, Asli Ozyurek, and Shiri Lev-Ari. The project will be implemented by a PhD student (1.0 fte, 48 months, see budget), together with a research assistant (0.2 fte until 31 August 2017, supported by Mirjam Ernestus, plus 1.0 fte, 24 months, see budget) and a post-doc (0.2 fte, 12 months, supported by Herbert Schriefers). This project will be integrated with closely related Lil projects, namely the project *"How to slow down and speed up: the regulation of speech rate"* - Joe Rodd (PhD student).

Project #2 will characterize multimodal and pragmatic alignment in dialogue. The visuospatial demands embedded in the coordination game will reliably evoke spontaneous multimodal utterances during the communicative interactions, despite the constraints imposed by the experimental setting (e.g. gaze and speech monitoring). This project will focus on those multimodal utterances, providing a sensitive window into the creation of shared representations in a format that is not available in speech^{26–28}. Accordingly, this project will provide an independent and fine-grained quantification of the relations between individual communicative signals and the shared cognitive space of the interlocutors, a quantification that is fundamental for a comprehensive characterization of alignment and highly relevant to the other three projects of this research program. The multimodal (this project) and the speech-related features of dialogic utterances (project #1) will also be used in formal Bayesian modelling of intention recognition²⁰⁻²². This follow-up portion of the project will characterize how the communicative choices of the interlocutors depend on the strength of their priors (e.g. presumed perceptual salience of a signal), distribution and "costs" of possible signals (e.g. biomechanical costs of a gesture, timing costs of articulation, literal semantic precision of a word), reliability of that sensory channel (e.g. environmental auditory noise), and constraints on the organization of the utterance (e.g. focusing on crucial information early in the utterance may facilitate the satisfaction of turn-taking constraints¹², whereas a uniform distribution of information would better satisfy information theoretic constraints²⁹). A number of pragmatic principles could be built into the model, for instance more complex signals may be set as more costly, testing whether this model parameter increases the descriptive accuracy of the empirical observations^{30–32}. This approach will provide formal descriptions of how linguistic features are selected within their domain. These domain-specific findings will provide important constraints for understanding how different linguistic features are integrated and aligned (Project #4). Furthermore, the corpus-based findings of Projects #1 and #2, and the bayesian modelling of communicative choices (this project) will also open the way for informed manipulations of the alignment dynamics. For instance, the degree of alignment of the interlocutors can be perturbed contingently on the presence of specific alignment markers, by introducing landmarks in one participant's map but not in the other, and by defining paths around different landmarks. This manipulation of the relative knowledge of the interlocutors is known to influence reliance on indirect speech acts (e.g. statements, questions, offers and pre-offers), as well as gestures and eye gaze, providing a tool for probing how different (para)linguistic features are used to re-align interlocutors' knowledge. It will also be possible to take into account socio-cognitive factors that could influence participants' ability to align their knowledge, e.g. properties of participants' social networks.

This project will be coordinated by Asli Ozyurek (responsible PI), in collaboration with a supervisory team constituted by Mark Dingemanse (co-promotor for the PhD project), Robert van Rooij, Raquel Fernandez, Stephen Levinson, and Harold Bekkering. The project will be implemented by a PhD student (1.0 fte, 48 months, see budget). This project will be integrated with closely related Lil projects, namely: "*Giving speech a hand*" – Linda Drijvers (PhD student), "*The Babel Problem*" – Luis Miguel Rojas Berscia (PhD student), and "*The Game of Language: Complex Communication and Mental States*" – Iris van de Pol (PhD student)

Project #3 will characterize the neurobiological mechanisms supporting the creation of a shared cognitive space across interlocutors and the corresponding alignment of linguistic features during dialogue. This project will simultaneously acquire neurophysiological markers of brain activity in both interlocutors ("hyperscanning"). These experiments are technically challenging, but feasible^{15,33} and important, given their ability to capture the interactive dynamics of mutual understanding in the interlocutors, rather than in actors or spectators³⁴. We plan to acquire electrophysiological markers of cortical activity (with EEG) during face-to-face spontaneous dialogue, and metabolic markers of cerebral activity (with fMRI) before/after performance of the visuospatial coordination game. The former approach will allow us to understand how addressees can anticipate the timing and content of a turn-end during turn-taking¹². The latter approach will allow us to understand how interlocutors align their representational spaces during a dialogue^{15,33}. For instance, by using representational similarity analyses of multi-voxel patterns, we can test whether interlocutors align their semantic, phonological, and gestural representations by using procedures involving the dynamic update of representational spaces through optimal pattern separation and pattern integration^{35,36}. Furthermore, the fMRI and (M)EEG data acquired in this project will be made available for the connectivity analyses on the brain organization that supports language implemented in the Big Question 2 (Figure 1).

This project will be coordinated by Christian Doeller (responsible PI), in collaboration with a supervisory team constituted by Ivan Toni, Steve Levinson, Pieter Medendorp, Jan Buitelaar, Asli Ozyurek. The project will be implemented by a post-doc (1.0 fte, 36 month supported by Lil and 12 months supported by Stephen Levinson). This project will be integrated with closely related Lil projects, namely: *"Modelling and mapping generalization and knowledge acquisition in the hippocampal-prefrontal-thalamic circuit"* - Stephanie Theves (PhD student), David Neville (WP2 post-doc); *"Flexible conceptual representations"* – Irina Simanova (WP4 post-doc); *"Neurocomputational mechanisms of communicative pointing"* – Tobias Winner (PhD student); *"Giving speech a hand: how functional brain networks support gestural enhancement of language"* – Linda Drijvers (PhD student); *"Neural processing of action, gesture and language in healthy and autistic individuals"* – James Truijllo (PhD student).

Project #4 will deliver a unifying theory that explains how semantic, phonological, and gestural features are integrated into one communicative signal. This project will develop a formal characterization of the computational problems faced and solved by interlocutors during a dialogue (in terms of input-output transformations²). By identifying the computational problem and formalizing possible solutions, this project will distinguish between a number of neuro-cognitive architectures that could (mis)align different linguistic features across interlocutors during a dialogue. For instance, integration between the linguistic features isolated in projects #1 and #2 could be based on feature-specific heuristics, largely ignoring conceptual information about the cognitive space currently shared across interlocutors^{8,10,37}. This scenario would afford a computationally lean but highly constrained alignment scheme, requiring direct interfaces between linguistic features with different signal/referent mappings (e.g. phonology vs. semantics). Alternatively, features integration might be based on inferential and generative processes (e.g. predictive processing³⁸, analogical reasoning for

incorporating the presumed knowledge shared across interlocutors^{39,40}. This scenario seems computationally more expensive, but it affords feature-specific communicative asymmetries without compromising overall conceptual alignment between interlocutors. Agent-based simulations of those formalizations can be compared to each other and to the empirical observations from the other projects to assess their relative strengths in explaining how human interlocutors communicate. Furthermore, it becomes possible to identify structural properties of the communicative situation that may lead to tractable computations^{15,31,32} or to computational bottlenecks (e.g. resource limitations that pose strong computational constraints on the formal theory).

This project will be coordinated by Harold Bekkering (responsible PI), in collaboration with a supervisory team constituted by Iris van Rooij, Ivan Toni, Jakub Szymanik, Mark Dingemanse, Johan Kwisthout, Steve Levinson. The project will be implemented by a post-doc (0.8 fte, 48 months supported by Lil and 0.2 fte, 48 months supported by Iris van Rooij). This project will be integrated with closely related Lil projects, namely: *"The Game of Language: complex communication and mental states"* - Iris van der Pol (PhD student); *"Flexible conceptual representations"* – Irina Simanova (post-doc); *"Neurocomputational mechanisms of communicative pointing"* – Tobias Winner (PhD student); *"Gestural enhancement of language"* - Linda Drijvers (PhD student); David Neville (WP2 post-doc).

7. Knowledge utilization

Knowledge obtained in this research program will be disseminated for societal use by using the instruments already made available by the Language in Interaction consortium. We foresee a number of domains in which the insights acquired by this research program could be relevant. For instance, knowledge of how interlocutors reduce the mismatch between their individual cognitive spaces can be used to improve performance in common automatic dialogue systems, such as Apple's Siri, Microsoft's Cortana, or Google Now. These systems often make use of statistical regularities present in a set of training exemplars, and link them to adaptive action selection procedures. However, to date, those automatic dialogue systems fail to capture and update the shared cognitive space that communicators expect to build during a conversation. Artificial cognitive agents might better satisfy human communicative expectations and improve their disambiguation abilities by using a cognitive architecture that continuously updates the conceptual space shared with an interlocutor. A major goal of this project is to define that cognitive architecture. Developing artificial cognitive agents that can generate and update a shared cognitive space with an interlocutor would result in a number of extraordinarily relevant applications. For instance, search engines on mobile devices might become able to use a dynamic conceptual frame to resolve intrinsically ambiguous signals produced by a user. It might also be possible to use the knowledge generated in this research program to tune artificial cognitive agents to the limited conceptual alignment produced by patients with Autism Spectrum (if that proves to be the case). This could lead to robotic agents producing and understanding communicative behaviours in a manner optimized to individual patient abilities, as well as artificial agents quantifying the updating of shared cognitive spaces for diagnostic purposes.

8. Research data management

Research data management will be done according to the RDM procedures and infrastructures of the Donders Institute and ILLC. Data of the multimodal corpus will be made available to the community by means of a dedicated website allowing for registered download⁴¹.

References

1. Everaert et al. (2015) Structures, Not Strings: Linguistics as Part of the Cognitive Sciences *Trends Cogn. Sci.* 19 729–743

2. Marr (Freeman, 1982) A computational investigation into the human representation and processing of visual information

3. Clark (Cambridge University Press, 1996) Using language

4. Levinson (Berg, 2006) On the human 'interaction engine' in *Roots of human sociality: Culture, cognition and interaction* (eds. Enfield et al.) 39–69

5. Gärdenfors (MIT Press, 2004) Conceptual Spaces: The Geometry of Thought

6. Gärdenfors (MIT Press, 2014) The geometry of meaning: Semantics based on conceptual spaces

7. Warglien et al. (2011) Semantics, conceptual spaces, and the meeting of minds Synthese 190 2165–2193

8. Pickering et al. (2004) Toward a mechanistic psychology of dialogue *Behav Brain Sci* 27 169–90

 Menenti et al. (2012) Toward a neural basis of interactive alignment in conversation *Front. Hum. Neurosci.* 6
 Pulvermüller et al. (2013) Motor Cognition–Motor Semantics: Action Perception Theory Of Cognition And Communication *Neuropsychologia* 55 71–84

11. Friston et al. (2015) Active inference, communication and hermeneutics *Cortex* 68 129–143

12. Levinson (2016) Turn-taking in Human Communication--Origins and Implications for Language Processing *Trends Cogn. Sci.* 20 6–14

13. Stolk et al. (2013) Neural mechanisms of communicative innovation Proc. Natl. Acad. Sci. 110 14574–14579

14. Stolk et al. (2016) Conceptual Alignment: How Brains Achieve Mutual Understanding *Trends Cogn. Sci.* 20 180–191

15. Stolk et al. (2014) Cerebral coherence between communicators marks the emergence of meaning *Proc. Natl. Acad. Sci. U. S. A.* 111 18183–18188

16. Enfield (2011) Sources of asymmetry in human interaction: enchrony, status, knowledge and agency *Moral. Knowl. Conversat.* 29 285

17. Dingemanse et al. (2015) Universal Principles in the Repair of Communication Problems *PloS One* 10 e0136100

18. Jaeger et al. (2013) Alignment as a consequence of expectation adaptation Cognition 127 57–83

19. Holler et al. (2015) Unaddressed participants' gaze in multi-person interaction: optimizing recipiency Front.

Psychol. 6 98

20. Blokpoel et al. (2013) A computational-level explanation of the speed of goal inference *J. Math. Psychol.* 57 117–133

21. De Jaegher et al. (2014) Game-theoretic pragmatics under conflicting and common interests *Erkenntnis* 79 769–820

22. van Rooij et al. (2015) Optimality-Theoretic and Game-Theoretic Approaches to Implicature in *The Stanford Encyclopedia of Philosophy* (ed. Zalta)

23. Anderson et al. (1991) The Hcrc Map Task Corpus Lang. Speech 34 351–366

24. Lickley et al. (2005) Alignment of 'Phrase Accent' Lows in Dutch Falling Rising Questions: Theoretical and Methodological Implications *Lang. Speech* 48 157–183

25. Prévot et al. (2015) A SIP of CoFee: A Sample of Interesting Productions of Conversational Feedback in 16th Annual Meeting of the Special Interest Group on Discourse and Dialogue (SIGdial) 149–153

26. Peeters et al. (2015) Electrophysiological and Kinematic Correlates of Communicative Intent in the Planning and Production of Pointing Gestures and Speech J. Cogn. Neurosci. 27 2352–2368

27. Galati et al. (2014) Speakers adapt gestures to addressees' knowledge: implications for models of co-speech gesture *Lang. Cogn. Neurosci.* 29 435–451

28. Tversky (2011) Visualizing thought *Top. Cogn. Sci.* 3 499–535

29. Jaeger (2010) Redundancy and reduction: Speakers manage syntactic information density *Cognit. Psychol.* 61 23–62

30. Galantucci et al. (2014) Do we notice when communication goes awry? An investigation of people's sensitivity to coherence in spontaneous conversation *PloS One* 9 e103182

31. Frank et al. (2012) Predicting pragmatic reasoning in language games Science 336 998

32. Stivers et al. (2009) Universals and cultural variation in turn-taking in conversation *Proc. Natl. Acad. Sci. U. S. A.* 106 10587–10592

33. Bogels et al. (2014) Conversational Interaction in the Scanner: Mentalizing during Language Processing as Revealed by MEG *Cereb. Cortex*

34. Silbert et al. (2014) Coupled neural systems underlie the production and comprehension of naturalistic narrative speech *Proc. Natl. Acad. Sci.* 111 E4687–E4696

. Collin et al. (2015) Memory hierarchies map onto the hippocampal long axis in humans *Nat. Neurosci.* 18 1562–1564

36. Milivojevic et al. (2015) Insight reconfigures hippocampal-prefrontal memories Curr. Biol. CB 25 821-830

37. Pickering et al. (2013) An integrated theory of language production and comprehension *Behav. Brain Sci.* 36 329–347

38. Kwisthout et al. (2016) To be precise, the details don't matter: On predictive processing, precision, and level of detail of predictions *Brain Cogn.*

39. Van Rooij et al. (2011) Intentional communication: Computationally easy or difficult? Front Hum Neurosci 5
 40. Blokpoel (Radboud Universiteit Nijmegen, 2015) Understanding understanding: a computational-level perspective

41. Son et al. (2008) The IFADV corpus: A free dialog video corpus Proc. Sixth Int. Lang. Resour. Eval.

BIG QUESTION 4

1. Big Question coordinators: Prof.dr. James McQueen & Prof.dr. Antje Meyer

2. Title of the Big Question

Variability in language processing and in language learning

3. Key words

Language skills battery; individual differences; genetic mechanisms; neural circuitry and plasticity; second-language learning; long-term memory schemata

4. Scientific summary of research proposal

We aim to characterize variation in language processing and learning skills and to determine how these variations relate to variations in the underlying biology of individual participants. The project has two strands: Strand A focuses on language processing skills in young adults, and Strand B on language learning skills in children and adults. Strand A will develop a comprehensive battery of language tasks targeting sound, meaning, and grammatical processing of words and longer utterances during speaking and listening. In addition, we will select or develop tasks assessing general cognitive skills that are likely to affect performance in language tasks. After extensive piloting, a demographically representative group of 1000 young adults will be tested on the battery. DNA will be obtained from all participants and used for genome-wide genotyping. About a third of the sample will also participate in neuroimaging studies in order to map the variation in neurobiology across the population. Advanced statistical modelling will be used to derive underlying core dimensions of linguistic ability, to situate each participant in a multidimensional skill space that maps population variation, and determine the manner in which these skills map onto structure and function of underlying brain circuitry. Integrating our new sample with Nijmegen's existing Brain Imaging Genetics cohorts, we will carry out focused investigations of genes and biological pathways that have been previously implicated in language ability, test how polygenic scores relate to performance on the task battery, and perform mediation analyses to bridge genes, brains and cognition. Strand B uses variability in learning ability to investigate why second-language (L2) acquisition

can become harder in adulthood. Do age-related differences in L2 learning reflect maturational changes in neural plasticity and in the schema-based mnemonic processes used for learning and consolidating linguistic knowledge and skills? We will examine age-related changes in the relative contributions of the medial temporal lobe and the medial prefrontal cortex and in the interactions between these pathways and the perisylvian language network. 360 children aged 8-17 and 360 adults from the Strand A sample will complete batteries of behavioural and neuroscientific tests on L2 learning. Analyses will seek to uncover associations between language-learning abilities and maturational changes in the brain and to characterize individual variability in these associations.

5. Composition of the project group

Name and title	Specialisation	Institution	Lil Work Package	Involvement
Prof. C. Beckmann	Computational methods for data understanding; structural and functional MR imaging	DCCN, U. Twente	6	Strand A and B host PhD student/ co- supervisor of Postdoc A3
Prof. H. Brunner	Genomics	Radboudumc, DCN	6	Strand A
Prof. J.K. Buitelaar	Developmental disorders, variability in cognitive functioning, imaging genetics;	Radboudumc, DCN	6	Strand A and B overseeing data collection, supervising Strand B projects
Dr. HR. Bosker	Speech perception, psycholinguistics	MPI	5	Strand A development of test battery, co-supervision of RA-A1
Prof. A. Cutler	Psycholinguistics, Speech processing and learning	UWS, Max Planck Institute	1	Strand A and B Advisor for development of test battery and learning materials
Prof. G. Fernandez	Cognitive neuroscience of memory	DCN/DCCN	2	Strand B Supervisor of PhD B1, Postdoc B1, and RAs B1-3
Prof. S.E. Fisher	Neurogenetics and functional genomics of speech, language and reading	Max Planck Institute, DCN	5	Strand A Supervisor of Postdoc A4: genetic analyses
Prof. B. Franke	Complex genetics, link to Cognomics Initiative/Brain Imaging Genetics (BIG) study and Nijmegen Biomedical Study	Radboudumc, DCN	6	Strand A Supervisor of Postdoc A4: genetic analyses
Prof. P. Hagoort	Neurobiology of Language	MPI and DCCN	3	Strand A supervision of Postdoc A2
Dr. R. Kessels	Neuropsychology	DCC, Radboudumc	6	Strand A
Dr. A. Marquand	Neuroimaging, machine learning, statistics	UMC, DCCN	6	Strand A, Advisor: Analysis strategies for normative data, collaboration with Postdoc A3 and RA-A1, RA-A2
Prof. J. McQueen	Speech recognition, learning about sounds and words in L1 and L2	DCC	1	Strand A and B Coordinator of Strand B, advisor for Strand A, and supervisor of PhD B1: overseeing development of learning tasks
Prof. A. Meyer	Psycholinguistics,	Max Planck	5	Strand A and B
	language production	Institute		Coordinator of Strand A and

List of consortium members of the project group

				supervisor of postdoc A1, advisor for Strand B
Dr. D. Neville	Mathematical psychology; modelling and data analysis; semantic and episodic memory interactions	DCCN	2	Strand B 0.3 fte Postdoc and supervisor of PhD B1
Prof. N. Schiller	Psycho- and neurolinguistics; electrophysiology of speech production	U. Leiden	1	Strand B
Prof. J. Vroomen	Psycholinguistics; sound learning; multisensory perception	U. Tilburg	1	Strand B

List of non-consortium members of project group

Name and title	Specialisation	Institution	Involvement
Dr. C. Francks	Genetics of complex human traits	MPI	Strand A Advisor: genetic analyses
Dr. E. Janse	Individual differences in speech comprehension	MPI	Strand A Co-Supervisor of Postdocs A1
Dr. G. Janzen	Memory; developmental psychology and cognitive neuroscience	BSI/DCCN	Strand B Supervisor of Postdoc B1
Dr. S. Jongman	Individual differences in cognitive control	MPI	Strand A Selection of general cognitive skills tests, supervision of RA-A2
Dr. K. Lemhöfer	Bilingual language processing, cognitive aspects of L2 learning	DCC	Strand B Supervisor of Postdoc B1
Dr. Rogier Mars	Neuroanatomy, neuroimaging, brain connectivity	DCC	Strand B Advisor: data analysis of structural imaging data
Dr. B. St. Pourcain	Genetic epidemiology	MPI	Strand A Advisor: genetic analyses
Dr. J. Udden	Neurobiology of language	MPI	Strand A Advisor: structural imaging work

6. Description of the proposed research within the Big Question

Our overarching objective is to characterize variation in language processing skills and in language learning skills and to determine how these variations relate to variations in the underlying biology of individual participants. The project has two strands, each with distinct goals. **Strand A** examines language processing skills in a large and demographically

representative sample of young adults (aged 18-30) and seeks to develop the first-ever comprehensive battery of language processing tasks that provides a fast and broad assessment of those skills. The behavioural measures from this battery will be related to neural and genetic measures. Rather than focusing on language processing, **Strand B** focuses on language learning skills, and it compares children (aged 8-17) with young adults (aged 18-30). Here the goal is not to produce a comprehensive characterization of variability, but rather to use variability to examine why age matters in second language (L2) learning: Why are some aspects of L2 easier to acquire later in life, and why are some individuals better at L2 learning than others? In spite of these differences, there will be considerable integration across the two strands. In particular, as described in more detail below, development of novel statistical approaches for analysis of large multi-level data sets will be shared across the strands, and a subset of the adults tested in Strand A will constitute the adult sample in Strand B.

Strand A: Variability in processing

Overview and objectives

Investigations of the psychological, social and biological foundations of human speech and language have largely ignored individual differences in the normal range of abilities. For decades, experimental research in this field has almost exclusively involved college students. In addition, most research has aimed to characterise the average performance of this limited pool of participants. Given such a narrow focus on average performance of college students, hardly anything is known about individual differences in language skills within this group, or among adult speakers and listeners more generally. Moreover, it is almost entirely unknown how variability in language ability across the population maps onto variations in brain structure and function or their genetic determinants. Charting the nature of such mappings is crucial for understanding the neurobiology of language, as well as disorders in which language function is impaired. Tracing out the connections between natural variability at different levels can provide novel insights into the underlying mechanisms, to complement findings from more traditional studies of developmental and acquired language pathologies. Thus, the long-term goal of the planned line of research is to characterise the variability in language skills in large demographically representative samples of young adults and chart the neurobiological and genetic underpinnings of the behavioural variability.

We focus on young adults (18 to 30 years) because studying their language skills is of obvious societal and educational importance and because the extensive available literature on the average performance of college students, who fall into this age-range, constitutes a useful background for research on a broader demographic.

To characterise variability in language skills, we must first develop a comprehensive battery of language tasks that is optimal for capturing individual differences in population samples. Many extensive batteries for language testing are available world-wide. We will carry out an extensive review of the literature and discuss the potential of these instruments with leading experts in the field, including the members of the Scientific Advisory Board. However, most batteries are directed at assessing language skills in non-native speakers or screening for language-related impairments (e.g. www.nederlandsetaaltest.nl; www.Pearsonassessments.com; www.pearsonclinical.nl). Such tests are unlikely to discriminate well between adult native speakers without impairments, with most individuals performing at ceiling. Therefore, a key

outcome from this project will be a Language-in-Interaction-Battery (LIB hereafter) comprising a set of tasks that (1) assess language skills comprehensively, (2) discriminate well between young adult L1 speakers, (3) are reliable, and (4) are fast and easy to administer, preferably via Apps or Web-based platforms. The LIB will initially be developed for Dutch participants, but we also aim to produce well matched versions of the battery in English, German and other languages, such that it will have a broad impact on the field.

Given the lack of prior work on natural variation in language abilities, there is no solid theoretical framework for designing tests that tap into core language skills. An important additional benefit of our work on LIB will be advances in developing such a framework. We will start by designing sets of tasks assessing different language strata (meaning, form and grammar) in processing of single words and longer utterances, in each case designing several tests for speaking and for listening (explained further below, and see Table 1). As speaking and listening draw upon domain-general skills, such as inhibitory control, working memory, and sustained attention, these skills will also be assessed, along with general intelligence. Factor analysis of the resulting array of performance indicators will be used to identify underlying dimensions of language skills. Thus, the project will contribute to a theory characterising the principal dimensions of language skills.

Defining these principal dimensions allows us to relate inter-individual variation in performance on cognitive tasks to variability in underlying aspects of brain structure, function and connectivity in language-related networks. To do so, we will develop a set of statistical models that encode brain-behaviour mappings linking the different domains of language function to underlying neurobiological circuitry ('normative models'). Such models will: (1) enable us to map the neurobiological underpinnings of language ability across all core domains of language skills and across the spectrum of functioning and (2) provide predictions at the level of individual participants, which will enable us to place each individual participant within the population distribution and thereby (3) map the neurobiological underpinnings of language ability at the level of the individual participant.

Studies of inter-individual variation in the general population can help uncover the genetic architecture underlying complex traits, giving molecular entry points into biological mechanisms. Variation in language-related skills is expected to have a multifactorial basis involving many genetic variants each with a small effect size. To yield adequate power in genetic association screening, the relevant phenotypes must be robustly characterized in large cohorts, an issue that has so far restricted advances in language genetics. Here, the development of the LIB, providing a novel research tool for rapid reliable large-scale assessments of language skills, will make a substantial contribution. In the long run, distribution of the LIB (and comparable versions in English, German etc.) to scientists who work with existing cohorts that are already genotyped (e.g., the Netherlands Twin Registry) will enable remote systematic phenotyping of language skills across multiple large datasets. This paves the way for future high-powered genome-wide association scanning via meta-analyses, facilitating state-of-the-art genetic epidemiology studies that evaluate the genomic relationships between different language-related traits, and their connections to cognitive and brain (endo)phenotypes, as well as identifying novel genetic pathways involved in language skills.

Contribution to the overarching quest of Language in Interaction

Language in Interaction aims "to account for, and understand, the balance between universality and variability at all relevant levels of the language system and the interplay with different cognitive systems, such as memory, action, and cognitive control". Strand A contributes to fulfilment of this mission in several ways. It addresses crucial, yet understudied, axes of variability: the variability in language skills among adult native speakers in relation to variability of activity in underlying neurobiological circuits and genetic architecture. The project will uncover how healthy adult speakers vary in language skills and begin to characterise the biological bases of this variability. Equally important, it will uncover invariances across speakers, both at the behavioural and at the neurobiological level, and will thereby contribute to our understanding of the constraints on the organisation of possible language systems. Moreover, the LIB will include tests of general cognitive abilities. Determining their importance for performance in a range of linguistic tasks will be a central concern. Similarly, the neurobiological studies will enable us to determine how variation in functioning in brain circuits involved in language relate to variations in language ability as well as in domain-general cognitive processes. Thus, the project will make an important contribution to a better understanding of the interplay of language and other cognitive systems. Finally, the LIB will facilitate large-scale studies of the genetic architecture underlying language-related skills using the state-of-the-art in genetic epidemiology, answering questions about domain specificity and generality from a unique molecular perspective.

Approach

The strand comprises the four sub-projects described below. The sub-projects have distinct aims, work plans, and well-defined responsibilities of the researchers. However, from the outset, there will be close consultation across sub-projects, in particular to make sure that the tasks developed in sub-project A1 are tailored to the needs of the neurobiological and genetic research projects and that the results can be analysed as envisioned in sub-project A3. A steering committee will be formed to make sure that the work in the various sub-projects is optimally co-ordinated.

Subproject A1: Development of the test battery (Postdoc A1, RA A1 and RA A2)

<u>Participants</u>. To develop and pilot the individual tasks, moderate sample sizes (around 80 participants) suffice. In order to obtain norms for the test battery, recruitment of a population-representative sample of approximately 1000 participants will be necessary. Participants must have basic Dutch reading, speaking, and listening skills, but need not be L1 speakers of Dutch. Dutch competence will be assessed through screening.

<u>Choosing language and general ability tasks</u>. Being able to characterize native language ability in terms of a set of core dimensions will be an important outcome of the project. However, as a provisional partitioning of language ability is needed to design the battery of tasks, we define 12 task domains by crossing (1) the linguistic stratum (sound, meaning, syntax), utterance type (word, sentence), and modality (production, comprehension). These domains undoubtedly overlap in the cognitive processes and brain circuits they engage. For instance, performance in many language tasks has been shown to be related to vocabulary size and inhibitory control. Determining how much the domains overlap will be a key outcome of the project. The current

plan is to devise tests tapping language skills at the word and utterance/sentence level. However, we will explore whether including tests tapping comprehension of text passages is beneficial.

Several tasks will be selected for each domain. For instance, the semantic component of word production may be assessed through picture naming, a synonym-production and an antonym production task. Table 1 provides further examples of tasks in each domain. The choice of tasks will be based on theoretical work (e.g., models of word production, auditory word recognition, sentence comprehension), a comprehensive survey of existing language test batteries and pilot testing. Because we intend to use the LIB for large-scale testing, in their final form the tasks should be short and easy to administer. Tasks that can be presented via Apps and/or Web-based platforms are highly preferred. To allow robust linking to neurobiological and genetic levels, the tasks must be highly reliable. Moreover, they must discriminate well within the group of young adults, and they should have good face validity (i.e. be plausibly related to everyday language use). The external validity of the battery will be established through its subsequent use in research and applied contexts.

Utterance type	Stratum	Production	Comprehension
Word	Semantic	Picture naming,	Lexical decision,
		Synonym production	Word recognition in noise
	Syntactic	Generating compounds	Lexical decision for compounds and
		and inflected forms	inflected forms
	Form	Precision of articulation	Sound discrimination
Sentence	Semantic	Free production (Type-Token	Self-paced reading,
		Ratio)	Click detection
	Syntactic	Sentence-picture matching,	Speeded grammaticality judgement,
		Scene description	Self-paced reading
	Form	Tongue twisters, Speech rate	Word recognition in context

Table 1: Example tasks for each domain

In addition to language skills, we will assess general cognitive abilities and some personality traits. Where possible we will use standardized or at least widely used tests, such as Ravens Matrices to assess general intelligence, the ANT to assess different components of attention, and digit span to assess working memory, as well as standardized questionnaires of Theory of Mind, Need for Cognition, and Reading Habits. As for the language skills, the choice of tools to assess general cognitive abilities and traits will be based on theoretical work, and surveys of existing test batteries and piloting. We will frequently consult with the members of the Scientific Advisory Board and other experts in the field.

Subproject A2: Determining neurobiological underpinnings of linguistic skills (Postdoc A2, RA A3).

The neurobiological infrastructure of language is also characterized by individual differences, for instance in the degree to which a direct connection via the arcuate fasciculus exists not only in the left but also the right hemisphere. In this part of the project we use structural MRI, resting state and task-based fMRI and Diffusion Weighted Imaging to determine the individual arrangements of the language connectome. Neuroimaging data will be acquired from about a

third of the sample recruited for norming of the test battery (i.e. ~360 people). We will focus on brain structure and morphology in language-related regions (e.g. perisylvian cortex and basal ganglia) and structural connectivity between the arcuate fasciculus, the longitudinal fasciculus, the extreme capsule, and certain other relevant fiber pathways in the left and right perisylvian cortices.

We will use protocols like those of the UK Biobank, the Human Connectome Project, and the Developing Connectome Project (for compatibility with those data sources). We will collect diffusion MRI data, T1 and T2 data, and five minutes of resting-state data. This will allow us to look at measures of white-matter integrity (using diffusion MRI), grey-matter structure and density (e.g. voxel-based morphometry), cortical thickness and areal expansion (using the T1 data), approximation of cortical myelin content (through T1/T2 ratio), and resting-state functional connectivity. These measurements are compatible with those proposed in BQ2 and match those in Strand B. Analyses can be based on established protocols using the Human Connectome Project processing pipeline.

In addition, a series of semi-standardized fMRI tasks tapping different aspects of comprehension and production will be conducted to extract and characterize individual activation patterns. These will then be fed into a normative modelling framework, as outlined below.

<u>Subproject A3. Data analyses and statistical modelling</u> (Postdoc A3, one PhD, one RA financed through Toolkit WP/Utilization WP)

Standard statistical tools can be used to determine the reliability of the tests of the LIB and to analyse the patterns within the behavioural data (regression, factor analysis). To map such behavioural data to variability in brain structure and function, it is necessary to map variation across the population and place each individual within the space defined by linguistic, cognitive and neurobiological dimensions. This is a normative modelling problem that is much more challenging than quantifying the mean difference between groups of participants and for which statistical techniques are in their infancy. We will capitalise on an innovative analytical methodology developed within the consortium. We will first use Bayesian regression methods to predict the full range of each of a set of biological response variables (e.g. regional brain activity) from a set of predictor variables relevant to language (Fig. 1A). This provides estimates of predictive confidence (error bars) for every prediction, allowing each point to be precisely positioned within the normative model. Centiles of predictive confidence can be interpreted as centiles within the normal range

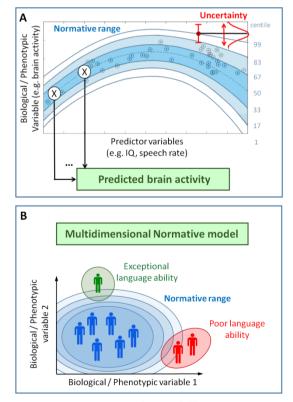


Fig 1: Normative modelling

(blue). By constructing normative spectra for all biological variables (Fig. 1B), we will derive a multidimensional distribution that characterises the full range of variation, linking all relevant predictor variables to each of the biological and phenotypic variables. This enables: (1) identification of outliers in the distribution, who may be individuals with exceptional or impaired language ability and (2) mapping of the nature of these deviations from the normative distribution at the level of individual participants.

Subproject A4: Genetic research

(Postdoc A4)

We will obtain DNA samples from all participants in the normative sample of 1000 phenotyped people using saliva sampling and perform genome-wide genotyping using standard single-nucleotide-polymorphism arrays. In parallel we will apply the LIB to existing cohorts available to our consortium, especially those where genome-wide genotype data and/or neuroimaging data are already available. One prominent example is Nijmegen's Brain Imaging Genetics (BIG) resource, which will by middle of 2016 include more than 2,700 participants for whom we have obtained genome-wide genotyping data coupled to structural MRI scans (along with other forms of neurobiological data). A web-based testing platform (iBIG2) allows new phenotypic data to be collected from BIG participants from whom we already have genotype and brain imaging data. The incorporation of LIB tests into the iBIG2 platform will facilitate genetic analyses of language skills in BIG.

The sample sizes of cohorts like our LIB normative sample and the BIG cohort are not sufficient for genome-wide association scans, but they can be used for more focused investigations of genes and biological pathways that have been implicated in language ability from prior research, for example from studies of disorders like speech apraxia, specific language impairment and developmental dyslexia. As well as studies of candidate genes and pathways, where possible we will make use of this knowledge base from prior literature to define polygenic scores for each individual and correlate those with language skills as indexed by LIB. Importantly, the availability of brain imaging genetics samples like BIG makes it possible to define how brain structure and function mediate the effects of genetics on language skills using mediation analysis. Finally, we will make the LIB available to collaborators who have existing genome-wide genotyped cohorts for use in remote phenotyping, which will facilitate large-scale meta-analyses with adequate power for identifying novel genetic effects on language skills.

Feedback from Scientific Advisory Board

- Question is extremely related to BQ4. Response: BQ4 and BQ5 have been combined.
- Many (huge) batteries on language available world-wide. Critically assess and use these where possible. *Response: This will be a major task of the first phase of the project.*
- Consult specialists on data collection and SAB once the proposal has been specified in more detail. *Response: We are more than happy to draw on our colleagues' expertise.* We will organise a workshop (mostly likely for March 2017) focussing on the selection of the tasks for the battery and on issues of data collection. All members of SAB as well as other experts will be invited. We may organise another workshop to discuss the results of the first phase of test development (approximately 18 months after the beginning of the project)
- How to dissociate language from other cognitive systems? Response: This will be one of

outcomes of the project.

- Testing words versus passages. Tests with kids are all about passages. Translational value. Response: The aim of the project is to develop a battery of tests that is fast to administer and taps core dimensions of language skills in a straightforward and transparent fashion. We will explore whether tests of text comprehension should be included. We expect the translational value of the project to be high, as the outcome should be a widely used test of adult language skills.
- Watch out for a bias towards risk-taking personalities when recruiting males in the police and army. *Response: We will consult with experts to make sure that we recruit a representative sample.*

Strand B: Variability in learning

Overview and Objectives

The ability to communicate linguistically is a unique human capability central to us as social individuals. Acquiring language is easier, more automatic and more successful early in life and becomes progressively harder, more effortful and less optimal as we age. For almost all of us, high proficiency is thus a given in our first language (L1) – and in any second language we are lucky enough to acquire early. But L2 learning in adulthood often presents difficulty. Why is language acquisition in childhood easier and why do individuals (children and adults) differ in their language learning ability? We aim to answer these questions using a novel, interdisciplinary approach that bridges the fields of L2 learning, psycholinguistics, human memory, and functional and structural neuroimaging.

The larger question here concerns how age-related neural maturation changes the way all languages are learned, native and non-native. We focus on L2 learning, however, for practical and theoretical reasons. Our interdisciplinary approach lends itself much better to the study of L2 acquisition in older children and adults than to the study of L1 acquisition in infancy and early childhood. A key part of our theoretical argument is that L2 learning is hard in part because the L2 is laid on top of an L1 with which it mismatches.

Many late learners have persistent problems with, to differing degrees, grammar, vocabulary (e.g. idioms), speech recognition in adverse listening conditions, and speech production (e.g. a noticeable foreign accent). L2 acquisition tends to get better the earlier someone starts learning¹, though there are exceptions (an estimated 5-15% of individuals attain native-like proficiency in a late-acquired L2²) and differences between linguistic domains (e.g. stronger age-of-acquisition effects for pronunciation than for vocabulary and grammar³). There is thus no strict Lennebergian maturationally-defined critical period (L2 acquisition closing at puberty). But there is a sensitive period: Age of acquisition is a strong predictor of attainment of L2 proficiency, especially for foreign accent^{3,4}, and for L2 processing⁵.

Our hypothesis is that age-related differences in language acquisition primarily reflect maturational changes (a) in neural plasticity and, relatedly, (b) in the neural pathways and schema-based mnemonic processes that support learning and consolidating new linguistic knowledge and skills. This hypothesis is grounded in the neuroscience of human memory.

The medial temporal lobe, with the hippocampus at its core, is the best-studied brain system involved in long-term memory^{6,7}. But this system appears not to be essential for language learning in childhood. In particular, hippocampal damage affects general knowledge and language acquisition in adulthood, but not during childhood and adolescence⁸. A second route into long-term memory must exist that is geared towards early-life plasticity. This second route, based on medial prefrontal cortex, has recently been discovered in adults. It enables formation and rapid consolidation of new memories, but only if the new information is related to existing knowledge represented in mental schemata^{9,10,11,12,13}. Evidence for a similar schema effect has been found for procedural skills; pre-existing manual motor skills enable better learning and consolidation of new sequential finger movements¹⁴. But the necessity of relatedness to preexisting knowledge or skills for use of the prefrontal memory route may be weaker during brain development because neocortex and especially prefrontal cortex appears substantially more plastic during childhood and adolescence than in adulthood. Knowledge and skill acquisition is better compensated for if neocortical damage occurs during childhood than if it occurs later in life. Furthermore, prefrontal cortex (in particular medial prefrontal cortex) has a protracted development lasting well into early adulthood¹⁵. This maturation is marked by transient overproduction of axons and synapses, peaking in early puberty, and by rapid pruning in later adolescence^{16,17,18}. Although the exact consequences of these changes are not well understood, it has been proposed that this neural remodelling fosters plasticity.

Our hypothesis is that this highly plastic, prefrontal neocortical route may be available – in the absence of fully-developed schemata – to assist in L2 acquisition during childhood and adolescence. We also hypothesise that this route will be able to help adults learn an L2 only if the structures in that language match the fully-developed schemata of the L1. The adult language learner may thus be confronted with a double whammy: existing schemata that do not necessarily fit the new language, and a neocortex that is much less plastic.

The medial temporal lobe and medial prefrontal cortex, we propose, together orchestrate in infancy, childhood and adolescence the formation, in perisylvian regions, of the mental structures that underlie language. In early adulthood medial prefrontal cortex becomes more mature and less plastic, making acquisition of another language harder because this prefrontal route can be used only for information related to already-existing schemata. This account assumes that prefrontal cortex plays a critical role in procedural and declarative aspects of language. Medial thalamic nuclei, connecting the medial temporal lobe to the medial prefrontal cortex, control memory generalization during encoding of specific episodic memories¹⁹, thus supporting declarative knowledge abstraction. The medial prefrontal cortex is not only well connected with the medial temporal lobe, but also with sensorimotor areas, associative cortices, and unimodal and multimodal representational areas, in particular the angular gyrus, known to be critical for integrating conceptual with perceptual representations²⁰ and combining concepts to form meaningful representations. Our hypothesis is that it serves this function in L2 acquisition.

Long-term memory representations supporting language processing exist in a broad network of interconnected regions in temporal, parietal and frontal cortex, primarily but not exclusively in the left hemisphere. While consensus has not yet been reached on all the details of this network^{22,23}, it is relatively uncontroversial that representations supporting the perception of

speech sounds are centred on the superior temporal cortex²⁴, those used in the recognition and production of the phonological form of spoken words and their syntactic properties are located primarily in the superior and middle temporal cortex^{23,24}, conceptual representations are in more inferior and anterior regions of temporal cortex and further parietal and frontal regions^{23,24}, and those supporting the production of speech sounds are in left inferior frontal cortex^{23,24}. These representations are spatially distributed across these regions and they work together dynamically (through fibre tracts such as the arcuate fasciculus) to support language comprehension and production²⁵.

This perisylvian network (together with structures in the basal ganglia) appears to support not only L1 but also L2 processing, though the relative involvement of different regions may vary in L2 processing as a function of age of acquisition^{5,26,27,28}. Different regions in the network appear to mature at different rates (e.g. the transverse gyri of auditory cortex appear to be established in utero and to have fully stabilized by age 7²⁹, while cortical thickness in the inferior frontal gyri in sequential bilinguals appears to depend on age of acquisition before versus after age 7³⁰). Importantly, the connections among these regions (e.g. the arcuate fasciculus) continue to develop into early adulthood³¹. Strand B's question, then, is whether age-related and individual differences in L2 learning ability depend on maturational changes not only in the medial frontal cortex and the medial temporal lobe but also in the perisylvian language network. Most fundamentally, the question is whether L2 learning ability depends on maturational changes in the interactions between the two pathways that support learning and memory consolidation and the network of long-term linguistic memory representations.

A defining feature of linguistic memory representations is that they must function to support language processing. Learning new knowledge about a foreign language is thus not only a question of acquiring that knowledge, but of integrating it with existing knowledge. Knowledge about new sounds need to phonologized, knowledge about new words needs to be lexicalized and knowledge about syntax needs to be grammaticalized. Memory consolidation supports this integration process (e.g. for new words^{32,33,34}). Strand B aims to examine whether there are age-related and individual differences in the way L2 knowledge is learned and consolidated. The focus will thus be on how new knowledge is integrated into an existing L2.

Another major initial motivation of this project was to take advantage of the fact that schemata – organized structures of knowledge in long-term memory – are well defined in the language domain. (Psycho)linguistic theory makes clear claims about the nature of the long-term memory representations of, for instance, speech sounds, lexemes, lemmas and concepts. We can thus test our hypothesis using well-specified schemata in a variety of different linguistic domains, including vocabulary, grammar and pronunciation. Equally importantly, we predict that results will vary across these domains because they have different developmental trajectories in L2 learning. L2 vocabulary acquisition appears to show little age-related decline, and appears to be based on the same processes that support L1 vocabulary acquisition^{35,36}. L2 grammar acquisition appears to become more difficult with age, but not all studies show such effects and there is evidence that adult learners can obtain native-like grammatical proficiency¹⁻⁴. L2 pronunciation appears to show the greatest degree of age-related decline³⁻⁴. A primary goal of Strand B is thus to compare these domains and ask whether these different trajectories and their neural correlates, just like the differences across individuals, provide insights into age-related changes in language learning ability. Furthermore, while schemata in the memory

domain have been considered to be associative in nature, those in language cannot be purely associative because they contain variables (e.g. phonological structures can be filled by different segments; syntactic structures can be filled by different morphemes). A key question will thus be whether our schema-based hypotheses will apply in the language domain. If so, this would show that schemata are richer than currently envisioned in the memory domain.

Originality and interdisciplinarity

This project aims to open windows into still largely unknown mnemonic processes and the neural representation of linguistic knowledge and skills. Its innovative nature is grounded in its interdisciplinarity, in particular the linkage between memory and language. There is a growing body of research on the role of schemata in memory⁹⁻¹³. Further, many studies have explored consolidation processes in language, particularly with respect to vocabulary acquisition^{32,33,34}. But no focussed attempt has yet sought to bring these domains together. The project is a two-way street, with the potential for discoveries about language, about memory, about their interaction, and about the nature of mental schemata. Another innovation will be to link in-depth analysis of the maturation of neural structures with age-related changes in language-learning ability. A good deal is known about developmental changes in grey- and white-matter density^{16,37} and connectivity³¹. These changes have begun to be linked to performance in L1³⁸, and there are indications, for example, that intensive L2 vocabulary training can influence hippocampal grey matter volume^{39,40}. But much remains to be discovered about how changes in memory and language networks relate to L2 learning ability.

Contribution to the Consortium's overarching quest

Everyone can learn an L2, but there are considerable differences in how successful people are, with age an important determinant of that variability. Strand B aims to uncover the ways in which maturational changes in the neurobiological underpinnings of language determine how well language can be learned. It thus lies at the heart of the Consortium's quest to understand the balance between universality and variability in the language system.

Approach

We will ask whether there are age-related changes in the relative contributions to L2 learning of the medial temporal lobe and the medial prefrontal cortex and in the interactions of these two pathways with the perisylvian language network. Given the lack of a clearly-defined critical period in L2 acquisition^{2,3} and considerable inter-participant variability among bilinguals matched in language exposure⁴¹, we assume a continuous model at the group level: that with increasing age L2 learning gradually becomes harder. It is of course also possible that there may be discontinuities within individuals (associated e.g. with the onset of puberty). The best empirical approach given this state of affairs is therefore not to define specific age groups in advance and compare them, but rather to rise to the challenge of collecting data from a large sample (360 children) covering a broad age range from well before puberty (age 8) until the point at which substantial maturational changes in medial prefrontal cortex have ended (age 30). We choose not to test older adults to avoid effects of age-related decline and because the adults will be tested jointly with Strand A (a subset of 360 adults from the larger Strand A sample). The sample will come from the Nijmegen population, including children from a wide

variety of schools from different parts of the city and adults from the university population and elsewhere (e.g. students in vocational training). The goal will be to obtain data from individuals who differ substantially in L2 ability. In this population, L1 is usually Dutch, and L2 is usually English, which is taught extensively in schools to a high level of proficiency, at least in those who continue to university. Many participants are expected to speak a third language (e.g., German, French), and some are expected to have learned Dutch as an L2 in primary school (having spoken e.g. Turkish at home before school age). As in Strand A, our approach is not to select specific ages or groups a priori, but rather to sample extensively from the local population. Groups (e.g. those with L2 Dutch; a specific age range) can nevertheless still be defined post-hoc.

Participants will complete batteries of behavioural and neuroscientific tests. First, we will construct a profile of individuals' abilities in English, using a battery of (where possible preexisting) behavioural tests (e.g. existing vocabulary and grammaticality judgement tests, proficiency ratings, degree of foreign accent and perceptual ability with hard-to-distinguish English phonological contrasts). Second, we will profile the participants as language learners. Individuals from the total sample will be divided into two groups (each with 120 children and 120 adults) and will each be asked to perform one of two child-appropriate language-learning tasks which probe different aspects of L2 learning: (B1) vocabulary: form and meaning, and (B2) grammar. These two language training tasks are described in more detail in the sub-projects below. Some training sessions will take place in the MRI scanner so that functional MRI data can be collected. Third, standard measures of Working Memory capacity, executive control, non-verbal IQ and Socio-Economic Status will be collected as (cognitive) control variables. For the adult groups, these data will be collected as part of project A1 described above. Results from a questionnaire on language experience and usage will be used as an additional control variable.

In addition to functional MRI during training, structural scans will be made. For the adult groups, this work is carried out in project A2 described above. For the children, we will use the same protocols. DNA will be obtained from the children as well.

Some within-participant measures will also be collected at a second time-point. These measures will include long-term retention of the material that was trained in the learning groups, and further structural MRI measures (to obtain longitudinal measures of structural changes). This work constitutes an important addition to the work carried out in A2.

We will create a 'neural fingerprint' of each participant which characterizes structural features that are hypothesized to reflect cortical maturation and contribute to L2 learning ability, such as cortical myelinisation, cortical thickness, and frontal-temporal connectivity (e.g. the arcuate fasciculus). We will examine in particular structures in the medial temporal lobe, the medial prefrontal cortex, the perisylvian language network, and connectivity among these structures. Comparisons can easily be made between participants and between time-points within participants⁴².

Data analyses and statistical modelling will use the same approach outlined under Strand A. Those analyses will aim to uncover associations (within time-points and longitudinally) between, on the one hand, language-learning abilities (from the training studies and the offline test battery) and, on the other, the neural fingerprints. We predict (1) age-related differences in the structures involved in learning different aspects of a new language (i.e. pronunciation/accent vs. vocabulary vs. grammar), and (2) weaker differences for information that is more easily integrated into existing knowledge, such as new words in a familiar language. It is also possible that we will discover neurobiological determinants of individual differences, such that adults who are better at L2 learning may have more "child-like" language brains. That is, there may be greater involvement of medial prefrontal cortex in such individuals than in those who find L2 learning hard.

Strand B will consist of two tightly interlocked sub-projects. The overall approach with respect to the set of behavioural and neuroscientific tests, as just outlined, will be the same for all 480 participants, and data analysis procedures will be shared too (also with Strand A). But the two sub-projects will be distinct with respect to the learning tasks in the two groups of 240 participants.

Sub-project B1: Word learning

This sub-project will focus on investigating the neurobiological underpinnings of conceptual knowledge accumulation and updating that underlies word learning. We will use a previously established artificial language paradigm⁴³ which is based on material developed by Kirby and colleagues⁴⁴. Participants will be trained to form higher-order associations between artificial words composed of syllables (i.e. 'NI-HE-KO') and abstract figures with a given colour, shape and movement (e.g. blue square moving to the left) that either fit or do not fit a learned structure (i.e., a schema). Behavioural performance will be analyzed via State-space modelling⁴⁵ to vield trial-to-trial estimates of: 1) the state of the underlying latent process (i.e. overall amount of information accumulated up to a given point in time) and 2) the amount of knowledge updating (i.e. amount of information acquired between two successive trials). These behavioural parametric estimates will be then used in conjunction with measurements of brain structure (i.e. white-matter integrity, grey-matter density, etc.) to test which feature of the 'neural fingerprint' is the best predictor of change in learning performance across ages or between different time points within a given subject. Functional MRI data will be collected to relate brain activity. connectivity and activation pattern during learning to changes in behavioural performance. Brain structures of special interest are the MTL, the mPFC, the DLPFC including Broca's area and the temporal/temporal-parietal area including the temporal pole and the angular gyrus.

Participants will take part in a multiple-day training protocol. On Day1, after stimulus familiarization, they will learn the word-figure associations in the MRI scanner and complete their structural scans. On subsequent days, they will be taught low frequency (i.e. previously unknown) L2 English words in a purely behavioural paradigm (based on prior work on word learning in adults and children^{32,33,34}). The words will be learned with associated pictures and definitions on Days 2 and 3 and tested for their integration into the English lexicon using a semantic priming task on Day 6. Critically, we will compare learning and integration/consolidation of the meanings of words with direct translation equivalents (e.g. English words for concepts for which the participants already have Dutch words, and hence have rich and well-established conceptual schemata) versus words without translation equivalents (e.g. English words for novel concepts with much weaker schemata, such as ancient agricultural tools, for which the participants do not have Dutch words). Performance on L2 vocabulary learning will be compared to the artificial word learning and the structural MRI

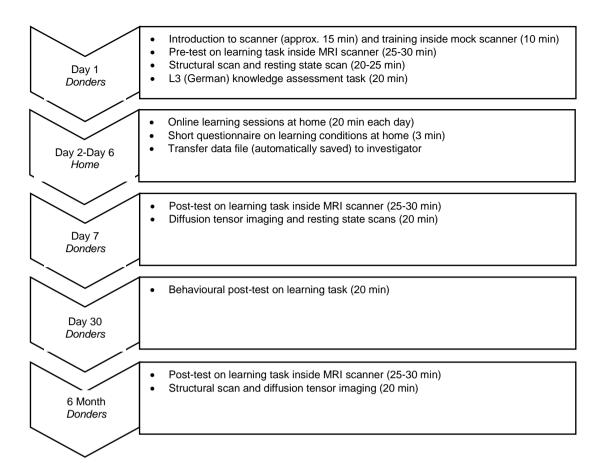
data. Long-term retention of both the artificial words and the English words will be tested 6 months later. Finally, participants will return one year after initial test to be scanned as they learn a further set of associations in the artificial word learning task and for a second structural scan.

The emphasis of this sub-project will thus rest on a well-controlled and model-based analysis of the neurobiological underpinnings of knowledge acquisition in the context of word learning and it will be geared towards testing hypotheses such as: 1) maturational changes in brain structure lead to a loss of plasticity and thus in the ability to accumulate new knowledge (e.g. a lower amount of or slower knowledge updating for older participants due to reduced mPFC maturation or connectivity), 2) the changes observed in the artificial word learning task are predictive of natural word learning in a second language as tested behaviourally.

Sub-project B2: Grammar

The aim of this study is to examine the development trajectory of the brain network specifically involved in grammar learning. To allow for the investigation of continuous development, we will make use of a correlational design and, as in the other sub-projects, test 120 children and adolescents aged 8 to 18 years and 120 adults aged 18- 30 years. Participants will be taught aspects of a natural grammar, namely German adjective declension ("Dies ist ein kleiner Mann / ein kleines Kind", 'This is a small man / a small child') that are not typically mastered by Dutch learners of German⁴⁶. German is an L3 in the participant population, usually acquired through formal classroom instruction. Whether the to-be learned feature is comparable to an existing syntactic feature in Dutch will also be manipulated by combining declension (which exists in Dutch) with case marking (which does not exist in Dutch), such as in the sentence "hier siehst du einen kleinen Mann", 'here you see a small man', 'a small man' in accusative). This will make it possible to test for an effect of schema compatibility. Learning and testing will take place in a child-friendly way using pictures and a simple grammatical decision task.

Behavioural pilot studies and a fMRI study are planned to investigate the relationship between behavioural improvements on the syntactic aspects and learning-induced neural plasticity changes. It will be investigated if and along which route learned novel grammar features are integrated into general grammar knowledge stored in long-term memory after time periods of one week, one month and six months. DTI scans will make it possible to investigate communication between different brain regions. This method allows us to examine whether density of white matter tracts predicts learning abilities in children. Resting state scans before and after training will investigate how the interaction between brain regions change with time. The figure below gives a schematic overview of the planned training study. Prior to the first day of training ("Day 0"), participants (like those in the other two sub-projects) will complete a battery of tests on L2 (English) proficiency measures and cognitive control measures (e.g. Working Memory, executive control, non-verbal IQ).



Feedback from Scientific Advisory Board

- There is a huge overlap with BQ5. Integrate BQ 4 and 5 into one big question on "variability" complementing each other. *Response: This integration has been done.*
- Where exactly is the focus of BQ4? Language models and how they change during development are missing (e.g. different trajectories for phonology and syntax). Some substructures and processes are addressed, but maturation of brain as a whole, and specifically language-related regions, is not sufficiently addressed. *Response: A few paragraphs have been added at the end of the objectives section to clarify (a) how we take into account the different developmental trajectories in L2 acquisition for different linguistic domains and (b) how we include the development of the perisylvian language network in our approach. We have also clarified that the focus will be on learning and consolidating new knowledge and skills into an existing L2 (rather than e.g. learning a completely new language).*
- The project seems more about memory than about language. How can language learning be separated from learning in general? *Response: As now clarified, a major initial motivation of this project was to take advantage of the fact that schemata are well defined in the language domain: (psycho)linguistic theory makes clear claims about the nature of the long-term memory representations of speech sounds, lexemes, lemmas and concepts. It is thus possible to test detailed hypotheses about L2 acquisition derived from memory research using well-grounded linguistic schemata. The project is thus not more about memory than language, it is about both, and it*

seeks to establish whether the mnemonic processes underlying L2 acquisition are or are not separate from non-linguistic mnemonic processes.

- Why the assumption of a linear decrease over age? Biological processes are almost never linear. *Response: The assumption, now more clearly stated, is that there will be a linear decrease with age at the group level. It is an empirical question whether this reflects linear or non-linear changes within individuals.*
- Natural language acquisition (immigrants) is different from learning at school (Dutch kids). This difference should be taken into account. It could be disentangled by using deaf children as subjects. *Response: We considered recruiting Deaf participants but chose not to do so given that we do not think it is feasible to find a large enough sample.*
- When interpreted as a developmental study, the proposed sample sizes need further specification. It's important to have sufficient subjects per age and sex to have enough statistical power. *Response: Sample sizes have now been specified.*
- Consider effects of puberty more. *Response: We sample across ages 8-17 so that it will be possible to compare pre- and post-puberty groups. We also intend to consult Evelien Crone (U. Leiden).*
- The NSA has 2 centres in the US where they collect data that is relevant to BQ4 (data on individuals with special aptitude for learning language). Although a long shot, it might be interesting to contact them about their database and know-how on this subject. *Response: This is indeed an interesting possibility which we intend to follow up.*

Research Plan: Strands A and B

Contributions of personnel

Strand A

Subproject A1: Development of LIB (Meyer)

- **Postdoc A1** (co-supervised with Janse)
- Research Assistant A1 (co-supervised by Janse and Postdoc A1 above)
- **Research Assistant A2** (co-supervised by Jongman and Janse)

Subproject A2: Neurobiological underpinnings (Hagoort)

- Postdoc A2
- **Research Assistant A3** (co-supervised by postdoc A2)

Subproject A3: Statistical modelling (Beckmann)

Funded through Toolkit WP: 1 Postdoc (A3), 1 PhD, 1RA (co-supervised by Marquand and Postdoc A3)

Subproject A4: Genetic bases of language skills (Fisher)

• Postdoc A4 (co-supervised by Franke)

Strand B

Sub-project B1: Word learning

• *PhD B1* (supervisors: Fernandez, McQueen, Neville, Postdoc B1)

- Research Assistant B1 (supervisors: Fernandez, Neville, Postdoc B1)
- Research Assistant B2 (supervisors: Fernandez, Neville, Postdoc B1)

Sub-project B2: Grammar

- **Postdoc B1** (supervisors: Lemhöfer, Janzen, Fernandez)
- **Research Assistant B3** (supervisors: Fernandez, Lemhöfer, Postdoc B1)

The entire Strand B team will work together in selecting (or where necessary piloting) the behavioural measures of L2 proficiency, designing the main study with children, and developing analysis procedures for the resulting data. There are nonetheless two distinct sub-projects. As itemized above, each sub-project will be supervised by overlapping teams (e.g. Postdoc B1 and Research Assistant B1 will contribute to both sub-projects). Each sub-project will be responsible for the development (design, materials) of its specific learning task and for running its group of 120 child participants (in close collaboration with the other sub-project). Each sub-project will also be responsible for analysing and reporting its own data.

Later in the project the personnel in the two sub-projects (in collaboration with Strand A and supported by Strand A research assistants) will test, analyse and write up the results with adult participants. In addition to the personnel mentioned above, Strand B includes advisors on study design, materials and data collection (Buitelaar, Cutler, Meyer) and on data analysis (Beckmann, Mars).

Organization and Timetable

BQ4 will organize meetings at three levels. First, the entire BQ team will meet three times a year to discuss overall goals, methods, organization and results. Second, each Strand will meet every two months to discuss planning and coordination at a more fine-grained level. Third, individual subprojects will meet on a regular basis (e.g. every week or fortnight) to discuss day-to-day activities (e.g. supervision of PhDs and RAs). A small steering committee will monitor progress and integration.

Period	Strand	Description	
Months 1-24	А	Create the Language in Interaction Battery, LIB, pre-test components	
Months 9-16	В	Selecting, constructing, and piloting tests and materials; designing main study	
Months 17-36	В	Test 360 children, aged 8-17: L2 proficiency tests, neural fingerprints and learning tasks (120 children per sub-project)	
Months 12-28	A&B	Develop statistical models that link behavioural measures to neural fingerprints	
Months 25-60	A	Test new sample of 1000 young adults on LiB, obtain DNA obtain LIB scores from participants in BIG	
Months 25-60	A&B	Test subset (360) of these adults: L2 proficiency tests, neural fingerprints and lear tasks (120 per Strand B sub-project); further develop statistical models that link behavioural measures to neural fingerprints	
Months 19-60	A	Conduct genetic studies into the basis of language skills	

Link to existing Language In Interaction projects and further embedding of the project

Strand A (especially component A1) will be embedded in ongoing work in Meyer's department at the Max Planck Institute, specifically research on individual differences in linguistic and general cognitive skills. Three researchers in the department (Jongman, Janse, Shao, all nonconsortium) currently contribute to this work. Particularly pertinent is the dissertation project by Nina Mainz (Development of vocabulary tests). A further PhD student working on a similar topic, also closely related to A1 will be hired in 2017. If the current project is funded, Jongman and Janse will devote 50% of their time to it. The department's project coordinator will also devote some of their time (up to 1 day a week) to the project.

Component A4 is closely linked to the research of the Language & Genetics department of the MPI (led by Fisher), which seeks to trace connections between genes, neurons, brains and language, as well as to the Radboud UMC's work on neuroimaging genetics (led by Franke). Much of the existing research of the MPI's Language & Genetics department focuses on language-related disorders, including the recently started Lil PhD project of Lot Snijders-Blok [WP5,6; supervised by Fisher & Brunner] which employs the latest next-generation DNA sequencing techniques to find rare causative mutations and identify new genetic pathways that could be relevant for language. Component A4 focuses on a complementary strategy for gaining insights using genetics, by studying the contributions of common gene variants to normal variation in language skills (and brain structure/function) in the general population. Data from Snijders-Blok's project and others at the L&G department can be valuable for helping direct the candidate gene/pathway analyses of component A4. This component will also take advantage of the expertise of non-consortium members, including Beate St Pourcain, expert in genetic epidemiological studies of population cohorts, and Clyde Francks, expert in genetic mapping of complex traits, both of whom lead research groups at the MPI.

Strand B is also connected to several ongoing Lil projects. These include Jana Krutwig's PhD project [WPs 1,7] and Lisette Jager's PhD project [WP1]. Both of these projects complement sub-project B3 because they are concerned with the relationship between speech perception and speech production in L2 learning. Jager's project in particular focuses on individual differences in phonological learning skill. Both projects use EEG techniques, which complement the MRI measures which will be used in Strand B. Shruti Ullas's PhD project [WP1] examines the neural underpinnings of speech learning and will interface especially with the work in sub-project B3. Strand B also connects with postdoctoral projects on word learning by Frank Eisner [WP1] and David Neville [WP2].

Strand B also takes advantage of the expertise of non-consortium members Gabrielle Janzen (on developmental cognitive neuroscience), Kristin Lemhöfer (on the psycholinguistics of bilingualism), and Rogier Mars (on neuroanatomy and brain connectivity). Janzen and Lemhöfer will supervise one of the sub-projects and advise Strand B more broadly on, respectively, neuroimaging in children and L2 acquisition. Mars will support data analysis.

Links to other Big Questions

Strands A and B are tightly interwoven with respect to shared personnel, shared data collection and shared data analysis. BQ4 as a whole also connects tightly to other Big Questions, both theoretically and practically. Structural MRI data collection for the 18-30-year-old participants, and aspects of the resulting data analysis, will be combined with BQ2. BQ2 will also contribute to our understanding of the language connectome in the human brain. There are further clear links to the computational issues addressed in BQ1 (e.g. mathematical modelling that links learning behaviour to underlying neural mechanisms). Data from BQ4 can be used for modelling in BQ1.

7. Knowledge utilization

This project will yield novel insights into the cognitive processes, brain circuits, and genetic architecture underlying speaking and listening and the processes and circuits underlying L2 acquisition. Strand A will yield descriptive data concerning the range of language skills in a large sample of young adult speakers. Such information should be of interest to bodies involved in developing teaching materials and assessment and diagnostic tools for young adults. The results from Strand B on L2 learning will have considerable societal relevance, particularly in Europe. The Strategic Research Agenda for Multilingual Europe 2020 states that tens of billions of Euros are spent annually on language translation, interpretation and learning. Understanding the ways in which age determines success in L2 learning can thus have substantial impact on language education.

We will disseminate our findings widely, for example through the Lil website, by attending relevant conferences, and through press releases and media appearances. We will also disseminate the findings to the language-teaching community (e.g. schools, teacher training institutions, makers of educational materials) through conferences attended by this community. We will create a large database comprising the results of all studies conducted during the project. This database will be freely accessible to the scientific community.

Finally, Strand A will yield the first version of the LIB. The project offers the opportunity to develop Web/App testing platforms that capture similar aspects of phenotypes to those used in the experimental studies, and to adopt those to overcome the power issue of complex genetic studies via remote phenotyping and meta-analyses of existing cohorts. We anticipate that the battery will be widely used and thereby cumulatively validated. In future work, we anticipate that the battery will be extended to other languages and developed for the assessment of children and older adults.

8. Research data management

We intend to use the data management system currently under development at the Donders Institute, with its protocols that ensure (a) ethical treatment of data (e.g. with respect to participant anonymity), (b) reliable and secure long-term archiving, and (c) open access to the data by the international scientific community.

Ethical approval for this programme will be obtained from the local ethics committee CMO regio Arnhem-Nijmegen (i.e. an acknowledged Dutch Review Board). Many of the data we propose to acquire fall under existing approvals for so-called standard studies held at the Donders Centre for Cognitive Neuroimaging (DCCN). These are defined as cognitive neuroscientific studies using EEG, MEG, (f)MRI, (f)NIRS, tCS/tACS and/or behavioural testing that do not apply any invasive intervention (e.g. medication) and include only healthy, legally competent adults (>18 years of age) as participants. Similar approvals have also previously been granted for the testing of children aged 8-17 with parental consent. All participants will provide written informed consent and will be informed that they are free to withdraw from the study at any time, that relevant insurance is in place and about the standard procedures for handling incidental findings (e.g. clinical abnormalities identified from the neuroimaging data acquired). All data will be anonymised and handled confidentially, securely and in full accordance with standard local procedures in addition to Dutch and European legislation. Where new DNA samples are collected this will be done using saliva-based kits according to the manufacturer's instructions. Saliva will be transported at room temperature to the RadboudUMC Department of Human Genetics and stored at room temperature until use. The samples will be labelled by a subject code number, study day number, state monitoring number, date and time of blood sampling. Neuroimaging data will be stored on secure file systems at the DCCN.

1 Johnson, J.S. & Newport, E.L. (1989). Critical period effects in second language learning: The influence of

maturational state on the acquisition of English as a second language. Cognitive Psychology, 21, 60-99. ² Birdsong, D. & Molis, M. (2001). On the evidence for maturational constraints in second-language acquisition. Journal

of Memory and Language, 44, 235-249.

³ Flege, J.E., Yeni-Komshian, G.H., & Liu, S. (1999). Age constraints on second-language acquisition. Journal of Memory and Language, 41, 78-104.

⁴ Birdsong, D. (2006). Age and second language acquisition and processing: A selective overview. Language Learning, 56 (s1), 9-49.

⁵ Ullman, M.T. (2001). The neural basis of lexicon and grammar in first and second language: The

declarative/procedural model. Bilingualism: Language and Cognition, 4, 105-122.

⁶ Scoville, W.B. & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. Journal of Neurology, Neurosurgery and Psychiatry, 20(1),11-21.

Squire, L. (1992). Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. Psychological Review 99(2),195-231.

⁸ Vargha-Khadem, F., Gadian, D.G., Watkins, K.E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory, Science, 277(5324), 376-80. ⁹ Tse, D., Langston, R.F., Kakeyama, M., Bethus, I., Spooner, P.A., Wood, E.R., Witter, M.P., & Morris, R.G. (2007).

Schemas and memory consolidation. Science, 316(5821), 76-82.

¹⁰ Tse, D., Takeuchi, T., Kakeyama, M., Kajii, Y., Okuno, H., Tohyama, C., Bito, H., & Morris, R.G. (2011). Schemadependent gene activation and memory encoding in neocortex. Science, 333, 891-895.

¹¹ van Kesteren, M. T. R., Beul, S. F., Takashima, A., Henson, R. N., Ruiter, D. J., & Fernández, G. (2013). Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: From congruent to incongruent. Neuropsychologia, 51(12), 2352-2359.

¹² van Kesteren, M. T. R., Rijpkema, M., Ruiter, D. J., Morris, R. G. M., & Fernández, G. (2014). Building on prior knowledge: Schema-dependent encoding processes relate to academic performance. Journal of Cognitive Neuroscience, 26(10), 2250-2261.

¹³ Spalding, K.N., Jones, S.H., Duff, M.C., Tranel, D., & Warren, D.E. (2015). Investigating the neural correlates of schemas: Ventromedial prefrontal cortex is necessary for normal schematic influence on memory. Journal of Neuroscience, 35(47), 15746-17551.

¹⁴ Müller, N.C.J., Genzel, L., Konrad, B.N., Pawlowski, M., Neville, D., Fernández, G., Steiger, A., & Dresler, M. (submitted). Motor schemas enhance procedural memory formation and protect against age-related decline. ⁵ Shaw, P., Kabani, N.J., Lerch, J.P., Eckstrand, K., Lenroot, R., Goqtay, N., Greenstein, D., Clasen, L., Evans, A., Rapoport, J.L., Giedd, J.N., & Wise, S.P. (2008). Neurodevelopmental trajectories of the human cerebral cortex. Journal of Neuroscience, 28(14), 3586-94.

¹⁶ Giedd, J.N., Blumenthal, J., Jeffries, N.O., Castellanos, F.X., Liu, H., Zijdenbos, A., Paus, T., Evans, A.C., & Rapoport, J.L. (1999). Brain development during childhood and adolescence: a longitudinal MRI study. Nature Neuroscience, 2, 861-863.

¹⁷ Andersen, S.L., Thompson, A.T., Rutstein, M., Hostetter, J.C., & Teicher, M.H. (2000). Dopamine receptor pruning in prefrontal cortex during the periadolescent period in rats. Synapse, 37(2), 167-169.

Andersen, S.L. & Teicher, M.H. (2004). Delayed effects of early stress on hippocampal development.

Neuropsychopharmacology, 29(11), 1988-1993.

¹⁹ Xu, W. & Südhof, T.C. (2013). A neural circuit for memory specificity and generalization. Science, 339(6125), 1290-1295.

²⁰ Wagner, I.C., van Buuren, M., Kroes, M.C.W., Gutteling, T.P., van der Linden, M., Morris, R.G., & Fernández, G.

(2015). Schematic memory components converge within angular gyrus during retrieval. eLIFE, 10.7554/eLife.09668. ²¹ Price, A.R., Bonner, M.F., Peelle, J.E., & Grossman, M. (2015) Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. Journal of Neuroscience, 35(7), 3276-3284.

²² Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. NeuroImage, 62(2), 816-847.

²³ Indefrey, P. (2011). The spatial and temporal signatures of word production components: A critical update. Frontiers ²⁴ Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. Nature Reviews Neuroscience,

8(5), 393-402.

 ²⁶ Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. Frontiers in Psychology, 4: 416.
 ²⁶ Archila-Suerte, P., Zevin, J., & Hernandez, A. E. (2015). The effect of age of acquisition, socioeducational status, and proficiency on the neural processing of second language speech sounds. Brain and Language, 141, 35-49.

²⁷ Palomar-Garcià, M.A., Bueichekú, E., Ávila, C., Sanjuán, A., Strijkers, K., Ventura-Campos, N., & Costa, A. (2015). Do bilinguals show neural differences with monolinguals when processing their native language? Brain and Language, 142, 36–44.

¹⁴², 30⁻⁴⁴.
²⁸ Román, P., González, J., Ventura-Campos, N., Rodríguez-Pujadas, A., Sanjuán, A., & Ávila, C. (2015). Neural differences between monolinguals and early bilinguals in their native language during comprehension. Brain and Language, 150, 80-89.

²⁹ Golestani, N., Price, C.J., Scott, S. K. (2011) Born with an ear for dialects? Structural plasticity in the 'expert' phonetician brain. The Journal of Neuroscience, 31(11), 4213-4220.

³⁰ Klein, D., Mok, K., Chen, J.-K., & Watkins, K. E. (2014). Age of language learning shapes brain structure: A cortical thickness study of bilingual and monolingual individuals. Brain and Language, 131, 20-24.

 ³¹ Brauer, J., Anwander, A., Perani, D., & Friederici, A. D. (2013). Dorsal and ventral pathways in language development. Brain and Language, 127(2), 289-295.
 ³² Gaskell, M.G. & Dumay, N. (2003). Lexical competition and the acquisition of novel words. Cognition, 89, 105-132.

³² Gaskell, M.G. & Dumay, N. (2003). Lexical competition and the acquisition of novel words. Cognition, 89, 105-132.
 ³³ Henderson, L. M., Weighall, A., Brown, H., & Gaskell, M. G. (2012). Vocabulary acquisition is associated with sleep in children. Developmental Science, 15, 674–687.

³⁴ Bakker, I., Takashima, A., van Hell, J. G., Janzen, G., & McQueen, J. M. (2015). Changes in theta and beta oscillations as signatures of novel word consolidation. Journal of Cognitive Neuroscience, 27(7), 1286-1297.
³⁵ Markson, L., & Bloom, P. (1997). Evidence against a dedicated system for word learning in children. Nature, 385, 813-815.

³⁶ Pajak, B., Creel, S. C., & Levy, R. (2016). Difficulty in learning similar-sounding words: A developmental stage or a general property of learning? Journal of Experimental Psychology: Learning, Memory, and Cognition, in press.
³⁷ Koolschijn, P.C.M.P., & Crone E.A. (2013). Sex differences and structural brain maturation from childhood to early adulthood. Developmental Cognitive Neuroscience, 5, 106-118.

³⁸ Skeide, M. A., Brauer, J., & Friederici, A. D. (2015). Brain functional and structural predictors of language performance. Cerebral Cortex. Advance access.

¹⁹ Mårtensson, J., Eriksson, J., Bodammer, N.C., Lindgren, M., Johansson, M., Nyberg, L., & Lövdén, M. (2012). Growth of language-related brain areas after foreign language learning. NeuroImage, 63, 240-244.

⁴⁰ Bellander, M., Berggren, R., Mårtensson, J., Brehmer, Y., Wenger, E., Li,T.-Q., Bodammer, N.C., Shing, Y.-L., Werkle-Bergner, M., & Lövdén. M. (2016). Behavioral correlates of changes in hippocampal gray matter structure during acquisition of foreign vocabulary. NeuroImage, in press.

⁴¹ Diaz, B., Baus, C., Escera, C., Costa, A., & Sebastian-Galles, N. (2008). Brain potentials to native phoneme discrimination reveal the origin of individual differences in learning the sounds of a second language. Proceedings of the National Academy of Sciences, 105, 16083–16088.

⁴² Mars, R.B., et al. (in press). Comparing brains by matching connectivity profiles. Neuroscience & Biobehavioral Reviews.

⁴³ Berkers, R., van der Linden, M., Neville, D., van Kesteren, M., Morris, R., Murre, J. & Fernández, G. (submitted). Neural dynamics of accumulating and updating conceptual knowledge.

⁴⁴ Kirby S, Cornish H, & Smith K (2008) Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. Proc Natl Acad Sci U S A 105(31):10681–10686.

⁴⁵ Šmith, A. C., Frank, L. M., Wirth, Š., Yanike, M., Hu, D., Kubota, Y., ... Brown, E. N. (2004). Dynamic analysis of learning in behavioral experiments. The Journal of Neuroscience, 24(2), 447–61.

⁴⁶ Davidson, D. J., & Indefrey, P. (2009). An event-related potential study on changes of violation and error responses during morphosyntactic learning. Journal of Cognitive Neuroscience, 21, 433–446.

BIG QUESTION 5

1. Big Question coordinators: Prof.dr. Roshan Cools and Dr. Andrea Martin

2. Title of the Big Question

The inferential cognitive geometry of language and action planning: Common computations?

3. Scientific summary of research proposal

The efficiency and flexibility with which humans infer (or generate) meaning during language comprehension (or production) is remarkable. How does our brain do it? To move beyond the many extant attempts to address this big quest, BQ5 will treat linguistic inference as an advanced solution to the multi-step, sequential choice problems that has been long faced in other cognitive domains (e.g. chess, foraging and spatial navigation). Specifically, BQ5 anticipates to make unique progress in unravelling the mechanisms of fast, flexible linguistic inference by leveraging recent major advances in our understanding of the representations and computations necessary for sequential model-based action planning. This approach will also lead us to revise current dual-system dogma's in non-linguistic domains, that have commonly over-focused on the contrast between a cognitive (flexible, but slow) and a habitual (fast, but inflexible) system: The current quest will encourage the integration of so-called 'cognitive habits' and their associated cognitive map-related neural mechanisms into theoretical models of both linguistic and non-linguistic inference.

We will leverage current rapid conceptual and methodological progress in our understanding of 'cognitive mapping' mechanisms for action planning (Behrens et al., 2018; Bellmund et al., 2018) to advance our understanding of how we generate meaning in the state space of language. In non-linguistic problems, the goal state is a function of the reward that is to be maximized. In the linguistic problem that we consider here, the goal state is the compositional meaning that needs to be generated during comprehension and production. Leveraging the recently developed approaches to understand action planning, we will contribute unique advances in our understanding of the neural code and computations that underlie the unbounded combinatoriality of language, i.e., the ease with which we can generate meaning.

4. Description of the proposed research within the Big Question

Overarching research question

The primary question is whether we can advance our understanding of language processing by generalising to the domain of language the inferential computations that use (and build) cognitive maps for spatial and non-spatial planning. Specifically, we aim to characterize the (similarities and/or differences in the) neural geometry of the cognitive maps for compositional language processing and action planning, as well as the computations over these cognitive maps for novel inference. As such we hope to identify the neural mechanisms of compositional linguistic structures, and those that unify or combine them (Dehaene et al., 2015; Hagoort, 2003), in relation to similar mechanisms in the domain of action planning.

A follow-up question is whether, as a result of putative computational commonality, the use of language can augment inference in non-linguistic domains, such as action planning, or whether linguistic primes can affect event perception and action planning. In this project we focus on the primary question, because the likelihood of providing an answer to the follow-up question depends critically on the identification of underlying common mechanisms.

Hypotheses

We will test and revise the hypothesis that inference across linguistic domains (for compositional meaning generation) and nonlinguistic domains (for e.g. compositional planning) relies critically on

1. The formation of, and operations over a *cognitive map*: Can we understand novel inference of linguistic meaning in terms of cognitive map-based behaviour, i.e. generative modeling of a novel route that represents a fast short-cut towards a goal location in an underlying abstract cognitive map?

2. The presence and integration of *multiple, separable knowledge maps*: a map of abstract structural relations (e.g. transition probabilities, grammatical relations or semantic relations) and a map of concrete sensory items (e.g. objects or words). One way to understand how an animal might take a new shortcut in real space is to consider that the statistical [abstract] structure of 2D space places strong constraints on which state transitions are possible. In the linguistic domain, we can ask whether an abstract, generalizable knowledge structure that is abstracted away from its sensory inputs (e.g. a grammatical relational structure or a semantic map), akin to grid cells in the nonlinguistic spatial case places constraints on what state transitions are possible in a more flexible map of relations between sensory inputs (i.e., words). Another way of framing this question is whether linguistic cognitive maps are populated by multiple relational structures that can be recombined as needed.

3. The presence of *successor representations* (Russek et al., 2017; Stachenfeld et al., 2017), which reflect predictive representations of the relationships between task states (i.e. a state is represented as a function of its successors), as opposed to an explicit map. This characteristic of the cognitive code for reinforcement learning and spatial planning lies at the interface of model-based and model-free control (Dayan, 1993). For this reason, successor representation might be particularly relevant for language. After all, generative modeling and inference of meaning during language processing is both flexible (like model-based control), yet also rapid and automatized (like model-free habitual control). We will ask whether we can understand flexibility and efficiency of novel inference in linguistic space in terms of saltatory leaping between shortcuts that are facilitated by the presence of successor representations in a map of abstract structural knowledge.

Team

Coordinators: The BQ5 team will be coordinated by Andrea Martin and Roshan Cools, who will seek regular consultation from Roel Willems, Branka Milvojevic, and Iris van Rooij. Roel, Branka and Iris have already acquired relevant experience from active participation in other ongoing Big Questions. Together they will ensure optimal streamlining and integration of the work that will be performed in five subprojects, in part based on the organization of regular meetings between all SP leaders. Please note that a variety of other experts have been consulted (for example,

Hartmut Fitz), as recommended in the previous board meeting, and we have included all those in the team who have expressed interest.

The division of the three key hypotheses across different subprojects reduces their interdependence. While all three hypotheses state that meaning generation relies on the presence and use of cognitive maps, we will test each of the specific hypotheses using a unique experimental paradigm.

The resources described below will be matched with co-funding from existing research groups, e.g. in terms of research/technical assistants. Embedding within these groups will ensure that adequate training opportunities are provided. Masters students will be recruited, e.g. from the CNS master's program, and PhD students from the International Max-Planck Research School on language.

Subproject 1: Neural geometry of language and action planning

SP1 will be led by Roshan Cools, Andrea Martin and Mona Garvert (principal investigators), who will collaborate with, and leverage expertise in language processing (Branka Milivojevic and Roel Willems), and artificial language programming (Jelle Zuidema) (co-investigators).

Functional MRI will be employed to investigate the commonalities and differences between the neural mechanisms for (i) cognitive map-based reward maximization during action planning and (ii) cognitive map-based meaning generation during sentence processing. This subproject will be implemented by a 4-year post-doc who will examine the first two main hypotheses of BQ5 by designing experimental paradigms that are matched as well as possible across the domains of action planning and sentence processing. To this end, we will train participants on novel sequences of events and words (i.e. an artificial language). This approach will enable us to examine whether the recent extension of 'cognitive mapping' to the conceptual domain (Behrens et al 2018; Bellmund et al 2018) can shed new light not only on model-based planning for reward maximization (Gershman and Daw, 2017) but also, more innovatively, on model-based reasoning for meaning generation.

This subproject will consist of two stages. First, we will investigate whether participants build and operate over neural cognitive map representations for both reward maximization and meaning extraction, evidenced by them taking novel short-cuts that they have never taken before. Second, we will investigate whether reward maximization and meaning generation are facilitated by constraints imposed by an abstract, generalizable knowledge structure that is abstracted away from its sensory inputs (e.g. a grammatical relational structure or a semantic map). Separating a representation of the relationships between states from the representation of the states themselves could be useful for generalising between tasks that follow a similar structure and thus greatly speed up learning (Behrens et al. 2018). To this end, we intend to translate experimental paradigms for assessing how multiple maps with the same abstract relational structure, but different sensory instantiations, are represented in the brain (Garvert et al., unpublished data, personal communication).

Subproject 2: Electrophysiological geometry of language and action planning

SP2 will be led by Andrea Martin and Roshan Cools (principal investigators), who will collaborate with, and leverage key reinforcement learning modeling and psycholinguistic expertise from Hanneke den Ouden and Roel Willems (co-investigators).

This subproject will be implemented by a 3-year post-doc who will examine the third main hypothesis of BQ5: Do we build and use successor representations for increasing the efficiency and flexibility of linguistic and nonlinguistic inference? We will adapt for EEG/MEG the spatial, non-spatial and linguistic experiments developed in WP1 to optimize them for identifying precompiled and time-compressed successor representations, i.e. (p)replay (Mommenejad et al., 2017). To this end we will leverage recent experimental work in the domain of model-based planning (Russek et al., 2017; Mommenejad et al., 2017) to investigate whether rapid novel inference for meaning generation requires not just a structural, invariant representations. EEG/MEG would be used instead of fMRI given that we anticipate their temporal resolution to be more optimized for isolating time-compressed sequences. Reinforcement learning modeling will be conducted to assess whether the operation of key 'caching' computations on the successor representations can account for the efficiency of post-scan reward maximization (in the nonlinguistic case) or meaning generation (in the linguistic case).

Subproject 3: Computing the inferential cognitive geometry of language and action planning

SP3 will be led by Andrea Martin (principal investigator) who will collaborate with Stefan Frank, Iris van Rooij and Jelle Zuidema, (co-investigators) in order to leverage computational modeling expertise in the domains of language and action planning.

SP3 will be implemented by a 3-year post-doc who will derive formalizations of the non-linguistic and linguistic experiments from SP1 and SP2, and then implement analogs of these formalisms in various neural network architectures. These neural network models will enable the specification of predictions for neurophysiological signals (for some types of computational models, at least), and to ascertain the fit of different representation types (e.g. high dimensional, vector, tensor, convolutional) to the neural response. Estimating the fit of these models will allow inference about the nature of neural representations underlying SPs 1 and 2. The crucial manipulation here will be whether the inclusion of temporal information in the neural network, including explicit temporal mechanisms for computation and time-compression information (whose neural basis will be investigated in SP1 and SP 2) improves the ability to perform the computational task analogs of the tasks that human participants performed in SP1 and 2, as well as providing a better fit to the neural data. Implementations that vary the timecourse of information availability and processing can be used to exclude possible mechanisms for (novel) inference in the linguistic and non-linguistic domain. Similarly, caching of the successor representations can be tested explicitly by using models that store successor representations and comparing them to those that do not. In the final phase of SP3, once the best-fitting models are identified, these specific architectures can be used to formalize the inferential geometry (or geometries) of action-planning and language, forming a model of how action-related and linguistic representations are encoded in the neural geometry (in accordance with both the neuroimaging data and performance of the computational models) and of how representations are composed on-the-fly during novel inference and compositional language processing.

Subproject 4: Inferential geometry of narrative spaces

SP4 will be led by Roel Willems and Branka Milvojevic (principal investigators), who will collaborate with, and leverage key psycholinguistic expertise in event perception from Monique Flecken (co-investigator).

Recent evidence supports the notion that we form cognitive maps for narrative content (Milivojevic et al 2015, Collin et al 2015, Milivojevic et al 2016, Manning et al 2018, Baldassano et al 2018). Nevertheless, a number of unanswered questions remain. One important question is what is the behavioural benefit of map formation. In SP4 we aim to determine whether the formation of narrative maps underlies story comprehension. Another question is whether the formation of narrative maps increases enjoyment of (and/or engagement with) stories through formation of successor representations of upcoming events (Silva et al 2019, Baldassano et al 2017). This subproject will be implemented by a 3-year post-doc who will examine the three main hypotheses of BQ5 in the narrative domain by leveraging naturalistic audio-visual stimuli, behavioural measures of narrative comprehension and enjoyment (Hartung, Hagoort, & Willems, 2017; Mak & Willems, in press), and state-of-the art (e.g. representational similarity) analyses of fMRI (Milivojevic et al 2015, Collin et al 2015, Milivojevic et al 2016, Manning et al 2018) and MEG (Schurmann et al, in prep) data. In our approach we examine whether the recent extension of the 'cognitive geometry' to the conceptual domain, can shed new light on situation model building during language comprehension (Zwaan & Kaschak, 2008). Narratives are ideally suitable stimuli to investigate this issue since they evoke rich situation model building and related immersive experiences in readers (Jacobs & Willems, 2017).

This subproject will consist of three stages which map onto BQ5's three main hypotheses. First, we will investigate whether narrative cognitive maps critically underlie inferences about narratives in terms of 'shortcuts' through narrative space as well as inferences about the underlying 'structure' of the narrative space (Hypothesis 1). We define 'shortcuts' as correct inferences about events which were not actually presented within the narrative (e.g. inferring the perpetrator), while we consider comprehension of 'story structure' to require correct inferences about the relationships between events (e.g. inferring the causality and temporal structure within the narrative). Second, we will investigate whether commonalities between the structure of multiple stories (in the form of event schemas or scripts; Schank & Abelson, 1977, Baldassano et al 2018) can be used to facilitate comprehension of similarly structured stories in terms of both 'shortcuts' about omitted events and the 'structure' of the latent story space, and whether the across-story commonalities are represented in separate neural circuits from those representing the relationships between story-specific events (Hypothesis 2). Third, we will investigate whether successor representations, here defined as predictions about the direction of the narrative, are generated during narrative perception (i.e. movie watching) (Hypothesis 3). An additional question we will answer is whether (violations of) those predictions (Silva et al 2019, Baldassano et al 2017) lead to increased memorability, greater engagement and increased enjoyment of the stories.

Subproject 5: Neurochemical mechanisms of inference for reward maximization and meaning generation

SP5 will be led by Hanneke den Ouden and Roshan Cools (principal investigators), who will collaborate with, and leverage key psycholinguistic expertise from Andrea Martin, Roel Willems and Branka Milvojevic (co-investigator).

SP5 aims to establish the commonalities and differences between the neurochemical mechanisms by which we make novel inference for reward maximization and meaning generation. We will focus on brain dopamine, because this neuromodulator is best established to be implicated in both model-based and model-free control of reward maximization and has also been shown to contribute to language processing (e.g. Tan, Cools, Hagoort et al, unpublished observations). The key question here is whether we can enhance rapid, flexible inference for meaning generation during language processing by enhancing dopamine-dependent model-based planning. SP5 will be implemented by a 4-year PhD student, who will set up, run and analyze a pharmacological MRI and/or MEG experiment using the paradigms developed in SP1, SP2 and/or SP4 (addressing hypotheses 1,2 or 3), depending on their progress. The dopamine system will be challenged with the most commonly used dopaminergic (and noradrenergic) drug, methylphenidate, as well as the neurochemically selective drug sulpiride. The onset of SP5 will be approximately 2 years after the onset of SP1 and SP4 and 1 year after onset of SP2.

	Year 1	Year 2	Year 3	Year 4
Subproject 1				
Subproject 2				
Subproject 3				
Subproject 4				
Subproject 5				

Workplan and timing of subprojects

References

- Baldassano, C., Hasson, U. & Norman, K.A., Representation of real world event schemas during narrative perception. J. Neurosci., 0251-18 (2018).
- Baldassano C, Chen J, Zadbood A, Pillow JW, Hasson U, Norman KA, 2017, Discovering event structure in continuous narrative perception and memory. Neuron 95, 709–721.
- Bellmund JLS, Gardenfors P, Moser EI, Doeller, CF (2018). Navigating cognition: Spatial codes for human thinking. Science.
- Behrens TEJ, Muller TH, Whittington JCR, Mark S, Baram AB, Stachenfeld KL, Kurth-Nelson Z. Neuron. 2018 Oct 24;100(2):490-509.
- Collin, S. H. P., Milivojevic, B. & Doeller, C. F. Memory hierarchies map onto the hippocampal long axis in humans. Nat. Neurosci. 18, 1562–1564 (2015).
- Dayan P 1993. Improving generalization for temporal difference learning: the successor representation. Neural Computation 5:613–624. doi: 10.1162/neco.1993.5.4.613
- Dehaene S, Meyniel F, Wacongne C, Wang L, Pallier C (2015). The neural representation of sequences: From transition probabilities to algebraic patterns and linguistic trees. Neuron 88, 12-19.
- Gershman SJ, Daw ND (2017). Reinforcement Learning and Episodic Memory in Humans and Animals: An Integrative Framework. Annu Rev Psychol. 68:101-128
- Hagoort P (2003). How the brain solves the binding problem for language: a neurocomputational model of syntactic processing. Neuroimage 20: S18-S29.
- Hartung, F., Hagoort, P., & Willems, R. M. (2017). Readers select a comprehension mode independent of pronoun: Evidence from fMRI during narrative comprehension. Brain and Language, 170, 29–38. https://doi.org/10.1016/j.bandl.2017.03.007

- Jacobs, A. M., & Willems, R. M. (2017). The Fictive Brain: Neurocognitive Correlates of Engagement in Literature. Review of General Psychology.
- Mak, H. M. L., & Willems, R. M. (in press). Individual differences in mental simulation during literary reading: Insights from eye-tracking. Language, Cognition and Neuroscience.
- Manning, J.R., Fitzpatrick, P.C. & Heusser, A.C., How is experience transformed into memory? bioRxiv. doi: https://doi.org/10.1101/409987 (2018).
- Milivojevic, B., Vicente Grabovetsky, A. & Doeller, C. F. Insight reconfigures hippocampal-prefrontal memories. Curr. Biol. 25, 821–830 (2015).
- Milivojevic, B., Varadinov, M., Vicente Grabovetsky, A., Collin, S. H. P. & Doeller, C. F. Coding of event nodes and narrative context in the hippocampus. J. Neurosci. 36,
- Russek EM, Momennejad I, Botvinick MM, Gershman SJ, Daw ND (2017). Predictive representations can link modelbased reinforcement learning to model-free mechanisms. PLoS Comput Biol.13(9):e1005768.
- Schank, R. C. and Abelson, R. P. (1977) Scripts, plans, goals and understanding: an inquiry into human knowledge structures. Lawrence Erlbaum Associates, Hillsdale, NJ
- Schapiro AC, Rogers TT, Cordova NI, Turk-Browne NB, Botvinick MM. Neural representations of events arise from temporal community structure. Nature neuroscience. 2013 Apr;1
- Silva M, Baldassano C, Fuentemilla L, 2019, Rapid memory reactivation at movie event boundaries promotes episodic encoding. biorxiv, doi: https://doi.org/10.1101/511782