Review

CellPress

Grounding language processing on basic neurophysiological principles

Angela D. Friederici[1] and Wolf Singer[2,3,4]

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Department of Neuropsychology, Leipzig, Germany
[2] Max Planck Institute for Brain Research, Frankfurt am Main, Germany
[3] Ernst Struengmann Institute for Neuroscience in Cooperation with the Max Planck Society, Frankfurt am Main, Germany
[4] Frankfurt Institute for Advanced Studies, Frankfurt am Main, Germany

In animal models the neural basis of cognitive and executive processes has been studied extensively at various hierarchical levels from microcircuits to distributed functional networks. This work already provides compelling evidence that diverse cognitive functions are based on similar basic neuronal mechanisms. More recent data suggest that even cognitive functions realized only in human brains rely on these canonical neuronal mechanisms. Here we argue that language, like other cognitive functions, depends on distributed computations in specialized cortical areas forming large-scale dynamic networks and examine to what extent empirical results support this view.

Neurophysiological principles that underlie behavior

Discussions on the biological basis of language as a human-specific trait have a long history [1–7]. Over past decades advances in neuroimaging techniques applicable to humans have provided highly consistent evidence on the functional specificity, location, and connectivity of language-relevant brain regions (for a review see [8]). With the exception of still scarce data from intracranial recordings, this evidence is mainly based on noninvasive imaging technology [MRI, magnetoencephalography (MEG), electroencephalography (EEG)] and therefore cannot be related directly to the underlying processes at the cellular and microcircuit level. However, comparative anatomical and electrophysiological studies across different species and various regions of the cerebral cortex provide compelling support for the notion that the computational algorithms realized in cortical networks are remarkably similar. These similarities comprise the biophysical properties of cortical neurons, the morphology and laminar distribution of excitatory and inhibitory subtypes of neurons, the organization of microcircuits, and the overarching principles of the connectome linking cortical areas [9–12].

The surprising stereotypy of cortical connectivity has led to the widely accepted notion of a 'canonical microcircuit', a connectivity motive that is preserved across species and different cortical areas [10,11]. Because the function of neuronal networks is determined by the properties of the constituent neurons and the specific circuitry mediating interactions, it is assumed that the neocortex always applies the same basic computational algorithm irrespective of the various tasks accomplished by different cortical areas. The specific functions accomplished by different cortical regions seem to be determined mainly by the input and output connections; that is, an area could receive its prominent input from and feed its output to either subcortical structures or other cortical areas. Strong support for this assumption comes from developmental studies showing that, by rerouting thalamic projections, visual maps can be formed in the auditory cortex and neurons in this region develop response properties similar to those normally found in the visual cortex [13]. These findings underline the pluripotency (see Glossary) of cortical computations and suggest that the specificity of functions depends on the embedding of an area in the brain's connectome rather than on its intrinsic organization. One of the conclusions derivable from this evidence is that the cortical areas supporting language processing should operate according to principles similar to those cortical areas dealing with sensory and executive processes in the non-language domain and therefore should be analyzable in animal models. Thus, the challenge is to understand the basic principles of cortical computation and to investigate to what extent these can also account for the complex cognitive processes realized in the human brain.

Here we take language as the test case. If the language faculty, one of the most complex cognitive functions, can be accounted for by common neurophysiological principles, this would be a strong case for the generality of these principles. We review neuroanatomical and functional

Glossary

Beam-forming techniques: beam forming is a signal-processing technique used to locate the sources giving rise to sensor signals.
Fractional anisotropy: a set of parameters describing the degree of anisotropy of water diffusion in axonal bundles. It is taken to reflect the density, diameter, regularity, and myelination of fiber tracts.
Hysteresis: the dependency of the output of a system on its activation history and not only on its current input.
Pluripotency: original meaning – the capability of a stem cell to differentiate into different cell types; meaning here – the ability of a neuronal network to fulfill different functions.
Segmental: any segment of speech that can be identified in the speech stream.
Suprasegmental: linguistic term denoting features of a sound or sequence of sounds beyond a single speech sound such as stress or pitch.

Corresponding author: Friederici, A.D. (friederici@cbs.mpg.de).

Keywords: language; oscillation; neural networks.

1364-6613/

http://dx.doi.org/10.1016/j.tics.2015.03.012

data relevant for speech and language, considering the different levels from single cells over microcircuits to large-scale networks. These data are compared with corresponding findings in non-language-related brain structures and non-language-competent species. An attempt is made to embed the human data in the framework of distributed coding in recurrent networks exhibiting high-dimensional dynamics (for a review see [14]). Here we argue that even the highly complex cognitive function of language is based on computational principles similar to those of other cognitive and executive functions.

In contrast to other means of communication, human language is distinguished by syntax, a system of rules and operations that permit the combination of information-carrying elements (words) into metastructures (sentences). Such syntactic structures allow the encoding of nested relations with their long-distance dependencies required for the representation of complex relations. They are not specific to the auditory modality as they are also incorporated in sign language [15]. Although there is some evidence that birds and monkeys are able to learn sequences following very simple syntactic rules, they are unable to cope with syntactically more complex hierarchical constructs [16–19] (Box 1). Because of this unique and modality-invariant property of the human language system to deal with complex hierarchical structures, studies on animal communication in nonhuman primates [16] and birds [20] have not led to the expected insights into language-specific processes, as discussed recently [21,22]. This difficulty to relate language-specific functions to neuronal processes may, however, be compensated by the fact that linguistic theory provides precise definitions of the basic features of linguistic units and of the most basic syntactic operations that underlie hierarchical syntax and thus the core of language [23] (Box 2).

Box 1. Sequence processing in different species

In a seminal and much discussed paper, the ability to process rule-based sequences was investigated across species [16]. It was shown that both humans and cotton-top tamarins were able to process auditory sequences following a simple rule, $(AB)^n$, but that only humans were able to deal with sequences guided by the more complex rule A^nB^n. Neuroimaging in humans revealed that only the more complex syntactic sequences of the A^nB^n type involved Broca's area, particularly BA 44 [126]. Interestingly, simple sequences of the $(AB)^n$ type activated a cortical region adjacent to Broca's area; namely, the frontal operculum, which is a phylogenetically older cortex [127,128].

Subsequent work in nonhuman primates [18] and birds [17,19] challenged the view that only humans can process complex rule-based sequences and applied sequences with more complex syntactic rules to these animals. However, these studies led to an ongoing discussion because of two aspects. First, it appears that these sequences are not comparable with the hierarchical structures of any natural language. Second, it has been argued that the birds' apparent ability to process syntactic rules [19] can be explained by much simpler, non-syntactic operations [20]. Thus, on the basis of the data currently available, it appears that nonhuman primates [16,18] and birds [17,19] can process non-hierarchical sequences, but not hierarchical structures as present in all natural languages [129].

Box 2. Linguistic units and language components

Language is more than a sequence of words. It comprises distinct linguistic units and rules combining these units. Different components of the language system are traditionally considered to deal with these units.

Phonemes and phonology. A phoneme is an abstract sound feature that makes the difference between two words (e.g., 'hat' versus 'cat'). These features and their combination are part of phonology. Another part of phonology is prosody, which deals with rhythm, stress, and intonation.

Morphemes and morphology. A morpheme is a word or part of a word. Morphology deals with the combination of morphemes into new words. There are inflectional morphemes that modify a word according to its role in a sentence (e.g., 'run–runs') and derivational morphemes that create new word forms (e.g., 'happy–unhappy'). Although inflectional modification is procedural (created by syntactic rules on each occasion anew), derivational creations are usually stored in the lexicon.

Lexicon. This is the store of all words (word forms) including their syntactic category (e.g., noun, verb) and respective meaning. Some theories assume that each word is associated with a bundle of semantic features (e.g., human, male) that are part of the meaning representation [130].

Syntax. This is a set of rules that guides the combination of words into phrases and sentences based on their syntactic category information. These have an inherent hierarchical structure reflecting the syntactic dependency between adjacent and nonadjacent words within or between the phrases in the sentences. A prominent theory assumes that there is a most basic syntactic operation, called 'Merge', that binds two elements (e.g., 'the', 'house') together into a syntactic hierarchy (with 'the' dominating 'house' in a syntactic tree) based on the category labels that each element carries (e.g., determiner, noun) [4]. By applying the operation twice, a larger phrase (e.g., 'to the house') can be built; by applying it multiple times, sentences can be built (e.g., 'The man ran to the house'). This operation is assumed to allow the build up of any structure in any natural language [23].

Neurons, ensembles, and distributed networks

Due to experimental constraints in recording single neurons or neuronal ensembles in humans, our information concerning the neural representation of basic linguistic units is limited [24–26]. However, data from nonhuman primates may provide basic information on how such units may in principle be represented at the neural level. The flexible combination of feature-specific neurons into neural assemblies is a strategy found in all sensory systems investigated in this review (visual [27], olfactory [28], auditory [29]; for a review of the principle, see [30]). Here we assume that the basic linguistic units such as phonemes and words are represented not by individual, highly specialized neurons but by small ensembles of temporarily cooperating neurons, each of these units being tuned to a component feature of the respective phoneme or word. By flexible recombination of these feature-selective neurons into different assemblies, a large number of phoneme combinations (words) can be encoded with a relatively small number of feature-selective neurons, like a nearly infinite number of words can be generated within each language with a small set of phonemes. Extrapolating further from evidence on the neuronal code for sequence processing in general, one expects that the processing of syntactic sequences and the binding of words into phrases and sentences is also accomplished by the generation of time-varying spatiotemporal patterns of distributed neuronal responses. Spatiotemporal patterns that represent phrases and sentences are and should be transient to deal with the infinite number of sentences made possible by the combinatorial character of language. The integration of syntactic and semantic information during sentence processing may be described as the activation of large numbers of neurons coordinated anew on each occasion [31,32].

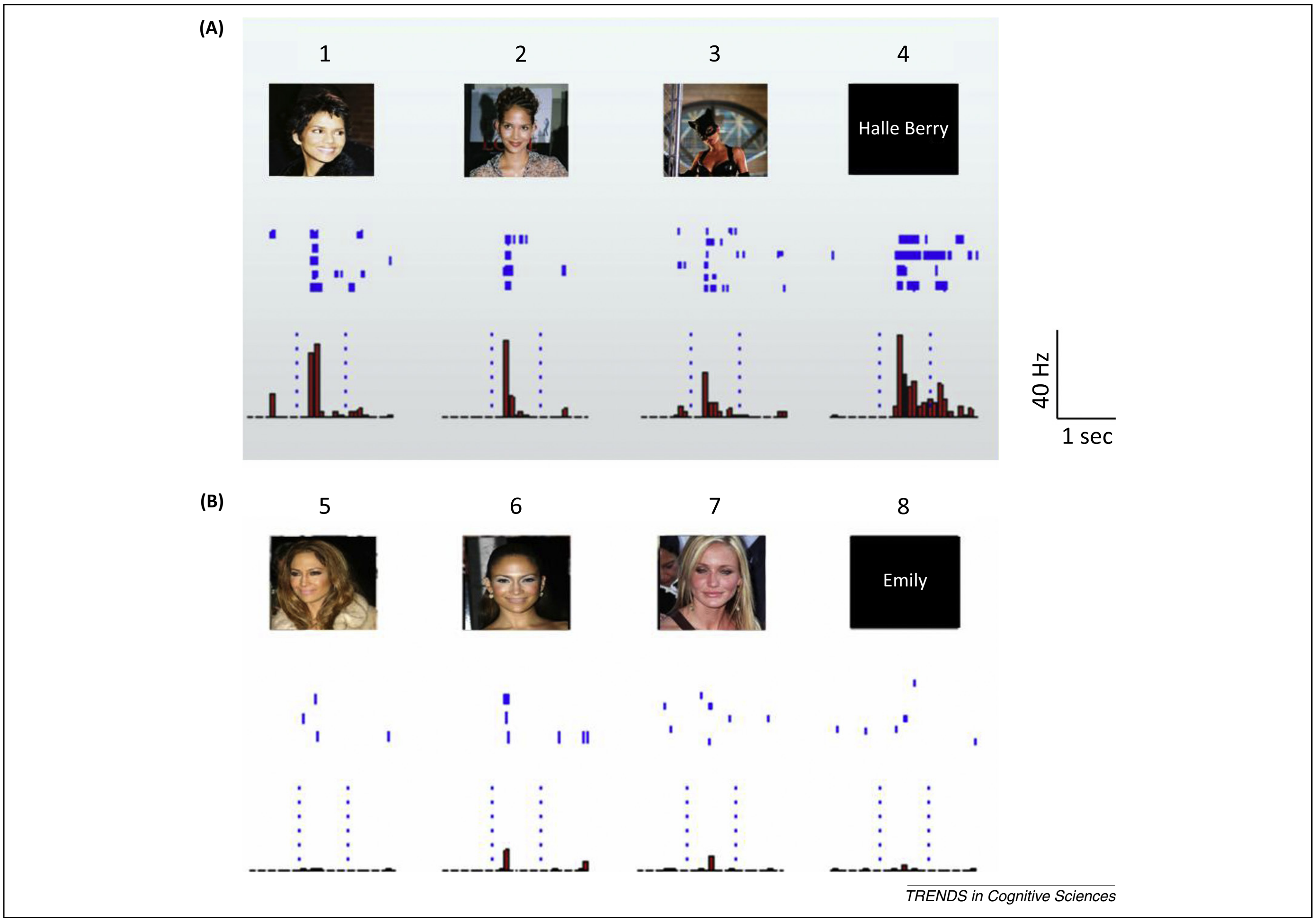
Single neurons in early sensory areas of the cerebral cortex are tuned to particular features of sensory objects (visual cortex [33], auditory cortex [34], somatosensory cortex [35]). However, when tested with complex stimuli these canonical responses also become more complex; that is, the receptive fields of the neurons change. The reason is that complex stimuli activate a large number of cortical neurons tuned to different features. Because of reciprocal coupling through excitatory and inhibitory circuits, all of the activated neurons influence one another and this results in complicated response dynamics [36,37]. It follows from these concepts of combinatorial distributed codes that individual neurons participate in different functional networks at different times. These networks, in turn, self-organize into functionally coherent assemblies on the backbone of anatomical connections depending on stimulus configurations and behavioral goals. When learning occurs in addition, the weights of the anatomical connections change, which in turn influences the association of neurons into functionally coherent assemblies. Accordingly, individual neurons function as multitasking units, as was documented recently in a study investigating the prefrontal cortex in nonhuman primates [38].

Processing language sounds

Similar distributed and dynamic coding strategies are likely to serve the representation of linguistic units. The few single-neuron studies from human subjects support this view. In medial frontal regions, cells have been found that are activated selectively in association with the articulation of vowels and, in the superior temporal gyrus, neurons have been identified that respond to simple, non-language-specific auditory features [24], and population signals have been found to correspond to more complex constellations of elementary features characteristic of distinct phonemes [25].

Processing semantic aspects

Semantic aspects appear to involve processing areas located in the medial temporal lobe (MTL) where some neurons were shown to be activated by a visually displayed object or a familiar person and her name [26], suggesting a high degree of conceptual abstraction at this level of processing (Figure 1). These findings have been interpreted as evidence for one crucial aspect of sparse coding; that is,



TRENDS in Cognitive Sciences

Figure 1. Single-unit recording. A single unit in the right anterior hippocampus that **(A)** responds to pictures of the actress 'Halle Berry' (1–3) and her written name (4). Three images of Halle Berry and the spiking responses to the images are shown. For each image, the corresponding raster plots and post-stimulus time histograms are given. Vertical broken lines indicate image onset and offset (1 s apart). Strikingly, this cell responds to photographs of Halle Berry, to her dressed as Catwoman, and to the letter string 'Halle Berry', but not **(B)** to photographs of other women (5–7) or another name (8). Adapted, with permission, from [26].

the representation of specific contents by a small number of highly specialized neurons [39]. Another aspect is that of temporal sparseness in neural responses. However, statistical considerations of the probability of encountering such units by chance indicate that even representations of highly abstract, modality-invariant concepts must still involve a large number of neurons bound temporarily into functionally coherent assemblies. This suggests that sparseness of coding is progressively achieved by iterative recombination of feature-specific responses along the processing streams that originate in the low-level, modality-specific sensory areas and converge in higher processing areas such as the MTL. Additional work has demonstrated that single neurons respond to semantic categories rather than to specific members of that category [26].

This latter finding can be directly related to cognitive theories modeling the relation between semantic memory and the representation of words. The assumption is that both semantic engrams and the representation of words share numerous common features (Box 3). Empirical support for the view that a word is represented as an ensemble of features comes from behavioral and electrophysiological studies. Thus, the time taken to recognize a word depends on the number of semantic features (semantic richness) [40] and brain responses vary as a function of the number of features by which a given word differs from prior context [41]. At the neuronal level, this would imply that a neuron representing a basic semantic feature may participate in various larger ensembles of word representations, with semantically related words being encoded by overlapping ensembles. Such a view would also be compatible with experimental data from language perception showing that the perception of semantically related words ('tiger' and 'lion') is facilitated when these are presented with a short delay, allowing preactivation of the ensemble representing the respective overlapping semantic features, but is inhibited when the related words are presented with no delay, leading to an interference effect [42]. This effect is probably caused by hysteresis of the ensembles encoding the overlapping semantic features. This time-sensitive interference effect has been located by means of MEG in the left temporal cortex [43], a cortical region known to be involved in the processing of semantic aspects at various levels of the semantic hierarchy [44]. Within such a hierarchy, names at a higher level are correlated with activation in the more posterior ventral occipitotemporal cortex, whereas basic-level names were shown to additionally activate the anterior–medial temporal lobe [45]. Future intracranial depth electrode recordings will have to provide the respective evidence at the neuronal level.

From these data we may conclude that neuronal representations for both phonemes and lexical items might combine sparse codes with the flexibility and combinatorial richness of assembly codes. Word forms are represented by assemblies of phoneme-specific cells that can be flexibly recombined to represent other word forms. Word-specific assemblies would then in turn be bound, on the one hand, with assemblies representing the various semantic connotations that activate respective sensory or motor regions for nouns and verbs [46]. On the other hand, they would become the units of temporally extended sequences of assemblies, bound together by syntactic rules and operations to represent sentences. The most basic syntactic operation that has been claimed to bind two elements into a syntactic structure is the operation 'Merge' [4,23], which, when applied multiple times, allows the building of any sentence structure in any language (Box 2).

The time-varying 'meta-assemblies' representing a sentence and closely related semantic meanings would in turn ignite other assemblies recruited from various subsystems of the brain, allowing the temporary build up of syntactic and semantic superstructures. Proving or falsifying this concept of hierarchical nesting of assemblies is, however, extremely challenging. Recently, nesting of oscillatory patterns with theta–gamma coupling for phonemic and syllabic processes has been described [47] (Figure 2). However, it is virtually impossible to simultaneously record the responses of all neurons temporarily bound into a given ensemble. It has been calculated that a given percept engages about 2 million neurons in the medial temporal lobe [48] and it is very likely that assemblies representing sentences and their semantic associations comprise similar numbers of neurons.

Box 3. Semantic features in semantic memory and lexicon

The relation between semantic memory and words represented in the lexicon has long been discussed in cognitive linguistics. According to some models, conceptual–semantic memory representations and the corresponding lexical–semantic representations can be described as ensembles of semantic features, with the word in the lexicon representing a smaller set of features [130] and the conceptual–semantic structure in memory representing a richer set of features [131–133]. The language-independent conceptual–semantic knowledge is traditionally thought to be represented in semantic networks [131] in which nodes represent particular semantic features of a concept (e.g., 'bird' has the features 'is animate', 'has wings', 'has feathers', 'can fly') and are arranged in a way permitting the encoding of hierarchical relations (with the category name 'animal' being higher in the hierarchy than the specific name 'canary'). For best use of words in communication, however, not all features need to be activated. For the correct use of the word 'bird' in a sentence (e.g., 'Birds fly') the activation of the semantic features 'animal', 'can fly' might suffice [130].

There are different views on semantics (see [134,135]) that are not discussed here. Rather, the present focus is on the feature-based semantic approach as it is of particular interest in the context of recent neurophysiological findings [26].

The dynamics within and between neuronal ensembles

It has been suggested that assemblies of temporarily bound neurons are characterized by enhanced coherence of the responses of the participating cells [49,50]. Coherence of small, spatially restricted assemblies appears to be assured by synchronization of oscillatory activity in the gamma frequency range (30–80 Hz) [43,51], whereas coherence in large, spatially extended assemblies appears to be established by synchronization of oscillations in lower-frequency bands (beta, 15–30 Hz; theta, 4–8 Hz). For a review see [52].

Processing syllables

Studies that focus on the neural dynamics of language processing remain rare. In the speech domain, it has been shown that the interhemispheric transfer between

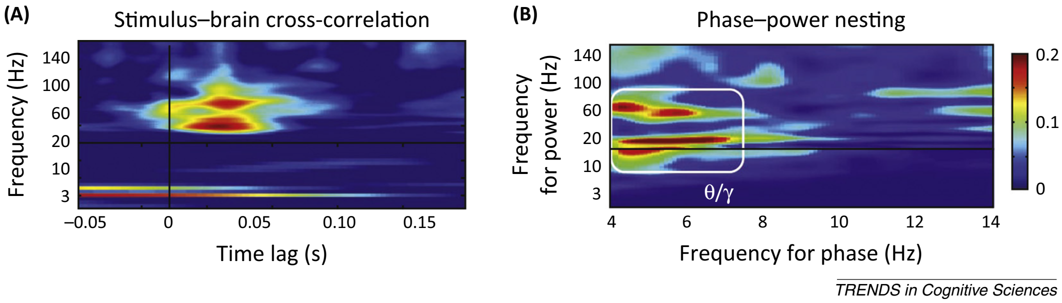


Figure 2. Nested oscillations. Speech–brain interaction from human intracortical recordings of primary auditory cortex. **(A)** Auditory cortex power strongly correlates with speech modulations in two frequency bands, theta and gamma. The theta band aligns to speech with zero time lag; the gamma band reflects speech modulations after a 40-ms time lag. **(B)** White box shows theta–gamma frequency nesting. Adapted, with permission, from [47].

primary and secondary areas of the auditory cortex during conscious syllable processing is based on synchronous gamma oscillations [53]. Focusing on recording from the auditory cortex, it was suggested that the Heschl's gyrus and the posterolateral superior temporal gyrus show a preference for a syllable compared with click trains [54]. Neural oscillatory activity as obtained by invasive electrocorticographic recording suggests left lateralized perceptuomotor processing in syllabic parsing [55].

Processing content words

The role of oscillations in the formation of word-related assemblies has been studied mainly in the context of memory formation and recall. Increased gamma oscillations (>30 Hz) were found when comparing content words (nouns and verbs) that carry semantic meaning to function words carrying no meaning [56]. Differences in gamma power were also reported for nouns and verbs reflecting different semantic associations such as visual scenes and motor acts, respectively [46]. Enhanced gamma oscillations were, moreover, reported when subjects processed semantic violations in sentences [57–60]. In tasks with high memory load or requiring extended search of stored information, coherence was increased in the theta range. Theta coherence within a large-scale network involving inferior frontal and temporoparietal regions was also found in semantic word–word priming for the coupling between the primer and the primed word [61] and when pseudowords had to be distinguished from real words [62]. Successful retrieval of words from memory was associated with enhanced coherence in the beta band between anterior and posterior brain regions [63,64]. These findings agree well with the notion that memory-related processes [65–67] and very extensive networks comprising widely distributed cortical areas are typically coordinated in the theta and beta frequency band [63,68,69].

Processing syntax

There are a few studies that have investigated oscillatory activity during sentence comprehension [70–73]. However, the investigation of syntactic aspects can be achieved only by disentangling these from other linguistic and non-linguistic aspects using either artificial grammar paradigms [74] or natural languages in which only syntactic parameters are varied systematically [75]. Such approaches have successfully been applied in the past in both event-related brain potential and fMRI studies (for a review see [8]). In a recent fMRI study on the processing of syntactically complex sentences, syntactic aspects were found to be located in the inferior frontal gyrus (IFG) whereas aspects of verbal working memory involved in the processing of such sentences involved the parietal cortex [76]. The spatiotemporal pattern underlying the processing of syntactically complex, memory-demanding sentences revealed left parietal alpha enhancement for the working-memory-intensive processing [75]. These results suggest the possible explanatory power of cortical dynamics at the level of sentential processing, and future research will have to show whether these promises hold.

A particularly fascinating finding is that oscillations of different frequencies coexist and exhibit phase–amplitude coupling, in which the amplitude of a fast oscillation varies with the phase of a concomitant slow rhythm [77]. It has been proposed that this phenomenon, known as cross-frequency coupling, might serve the encoding of nested relations whereby the assembly oscillating in the low-frequency range is thought to represent a supraordinate content (e.g., a category) while the fast-oscillating assemblies nested within the slow rhythm represent more specific items (for a review see [78]).

Small-scale and large-scale networks

The size of functional networks defined by synchronous activity covers many different scales. Accordingly, methods for their identification differ. Small-scale, local networks are usually identified by measuring the power of local oscillatory signals known as local field potentials (LFPs) when recorded with invasive techniques or as sensor signals when recorded with EEG/MEG techniques. The reason is that the power of these signals increases with the number of neurons participating in a synchronous assembly and with the precision with which neurons are synchronized among each other. Large-scale networks that usually extend across several cortical areas are identified by determining the synchronicity and/or coherence of oscillatory signals picked up from different electrodes or sources identified with beam-forming techniques. Using coherence measures, large-scale networks have been identified for numerous cognitive and executive functions. They form and dissolve in a transient context- and goal-dependent way and often reflect well the density of anatomical connections between the respective cortical areas, or nodes.

Sound attributes of language

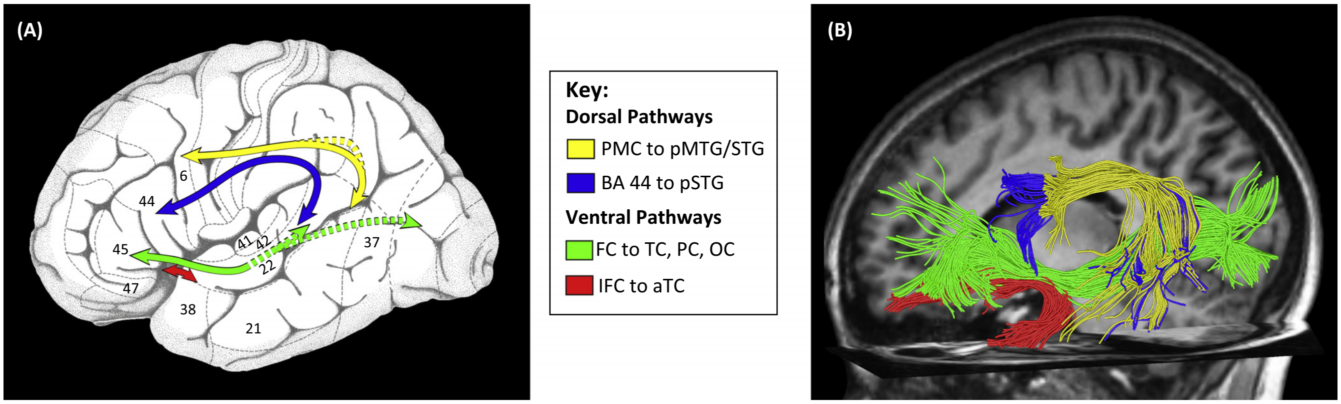
Speech sounds and prosody concern the segmental and suprasegmental aspects of spoken language, respectively. The former aspect is dealt with by a local network in the left hemisphere, whereas suprasegmental information is mainly processed in the right hemisphere. The differentiation between speech and non-speech is accomplished by a network in Heschl's gyrus and directly adjacent regions and the differentiation between various aspects of speech sounds (frequency, spectral information) is computed in a region lateral to Heschl's gyrus at the convexity of the superior temporal gyrus extending into the superior temporal sulcus, the planum temporale [79–81]. To encode segmental information, the system must operate with a temporal resolution of 20–50 ms, whereas a temporal resolution of 150–300 ms is sufficient to cope with suprasegmental information. If oscillatory patterning of responses were used for temporal parsing, this should imply that segmental and suprasegmental information is parsed by oscillations in different frequency ranges. In accordance with the hemispheric specializations for speech functions, it has been proposed that the left and right hemispheres preferentially operate in these different time domains; that is, the left hemisphere in the gamma range and the right in the theta range [82,83]. When processing connected speech, however, segmental information processed in the left hemisphere and larger-scale suprasegmental information processed in the right hemisphere [84,85] must be integrated. The bihemispheric network dynamics underlying this integration during speech perception as a whole remain to be described at the neural level.

Semantic attributes of language

Functionally, a modality-independent representation of semantic knowledge (as tested with pictures, symbols, and words) has been located in the anterior temporal lobe [86]. Investigations of the neuronal mechanisms engaged in the storage and read out of lexical–semantic representations have so far remained confined to the macro level and were based either on patient data [87] or on fMRI [88] approaches. These studies suggest a widespread semantic network involving temporal and parietal regions as well as inferior frontal regions. Temporal and parietal regions, particularly the angular gyrus [Brodmann area (BA) 39] and the supramarginal gyrus (BA 40), as part of Wernicke's area are supposed to support the storage or representation of lexical–semantic information [89,90] as well as sentence-level processes such as the establishment of the relation between the verb and its arguments [91,92]. The inferior frontal regions, particularly the pars triangularis (BA 45) and orbitalis (BA 47), appear to serve its retrieval and manipulation [93,94]. This suggests again that local, small-scale networks cooperate in a large-scale network that extends across several cortical lobes when lexical–semantic information is accessed and processed in the human brain. These regions are structurally connected by ventrally located fiber tracts; namely, the uncinated fascicle and the extreme fiber capsule system, also called the inferior fronto-occipital fascicle [95] (Figure 3). The brain regions together with the fiber tracts constitute the semantic processing system. However, this is not unique to the language system. The networks involved in the representation of polymodal sensory objects and in the control of attention are equally widespread (for a review see [96]). One basic theme appears to be that functional networks are formed dynamically on the backbone of the anatomical connections by enhancing the coherence of temporally structured activity (see [96]).

Syntax

Syntax concerns the set of rules according to which complex structures are generated. However syntax, although complex, can be broken down into very basic principles [23,97] (Box 2), possibly allowing a more fine-grained neural grounding than has been resolvable so far [98]. The neural substrate for the processing of syntactically complex sentences comprises a large-scale frontotemporal network involving the left IFG and the left posterior superior temporal gyrus and sulcus (pSTG/STS) [99]. The basic operation of 'Merge', by contrast, appears to be localized in a very



TRENDS in Cognitive Sciences

Figure 3. Language-relevant fiber tracts. **(A)** Systematic view; **(B)** anatomical view. There are two dorsally located pathways and two ventrally located pathways. The dorsal pathway connecting the dorsal premotor cortex (PMC) with the posterior temporal cortex [the posterior middle temporal gyrus and sulcus (pMTG/STG)] involves the superior longitudinal fascicle (depicted in yellow); the dorsal pathway connecting Brodmann area (BA) 44 with the posterior STG involves the arcuate fascicle (depicted in blue). The ventral pathway connecting the inferior frontal cortex (FC) – that is, BA 45 and others – with the temporal cortex (TC), parietal cortex (PC), and occipital cortex (OC) involves the inferior fronto-occipital fascicle (also called the extreme capsule fiber system); the ventral pathway connecting the anterior inferior FC (IFC) – that is, BA 47 and the frontal operculum (FOP) with the anterior TC (aTC) involves the uncinate fascicle. Adapted from [95].

confined region; namely, in the pars opercularis (BA 44) in Broca's area, suggesting a small-scale network [100]. This organization closely resembles that of other sensory/motor systems. Here, too, areas with highly specific functions exhibit little variability with respect to size and location.

For the processing of sentences, the small-scale syntactic network in the left BA 44 works together with a syntax-related working memory system located in the left inferior frontal sulcus. These two regions are connected by short-range white matter pathways and exhibit functional coupling during the processing of complex syntactic hierarchies [100]. This small-scale network is part of a large-scale network that in addition involves posterior temporal and parietal lobes [101]. This larger network exhibits functional coupling of frontal and posterior regions during sentence processing [102,103]. Structurally these cortical areas are connected via dorsally located long-range white matter fiber bundles – the arcuate fascicle and the superior longitudinal fascicle – and are functionally coupled during sentence processing [102,103] (Figure 3). The structural features of these fiber tracts, which can be derived from fractional anisotropy in diffusion tensor imaging (DTI), are highly correlated with the processing of verbal memory-demanding, syntactically complex sentences in adults [76] and the increasing processing success with such sentences during childhood [104].

The involvement of a dorsal and a ventral processing stream for language in humans so far has been discussed mainly on the basis of functional data [105–107] rather than structural data [104]. The general organizational features of the two processing streams closely resemble network organizations in the non-language domain. For instance, the visual system also contains large networks, also called processing streams, that comprise occipital, parietal, and temporal regions. The dorsal stream processes object attributes required for the control of grasping movements whereas the ventral stream analyses the features required for object recognition [108]. In both nonhuman primates and human subjects, these areas occupy the same subdivisions of the occipitotemporal cortex [109,110]. This suggests genetic determination of wiring patterns that predispose cortical areas to take over specific functions. These functions are then optimized during development by experience-dependent pruning of connections and subsequently refined by learning processes.

Network complexity

The architecture of cortical networks at both the functional and structural level has been optimized by evolution for complexity. Network complexity is lowest when connections between nodes are either highly regular, like the edges between atoms of a crystal, or completely random. Somewhere between regularity and randomness is an optimum where complexity – and hence the amount of information contained in the network – is maximal. Graph-theoretical analyses suggest that cortical networks are close to this optimum [111,112]. Interestingly, evolutionary studies based on species comparison indicate that phylogenetically recent brains (nonhuman primates and humans) show the highest degree of complexity [11]. Moreover, they indicate that human brains differ from those of their nearest neighbors by the emergence of nodes that have an exceptionally high degree or number of edges/connections with other nodes. Relevant in the present context is the fact that these strategic hubs are all related to networks supporting the highest cognitive functions such as polymodal integration and the integration of semantics and syntax in language. This emergence of highly interconnected hubs may be intimately related to the evolution of language competence. As these motifs of the connectome show little interindividual variability within a given species, it must be assumed that they are genetically specified.

Our knowledge about cortical networks has been increased by DTI, which allows one to describe the structural connectivity between different areas in the human brain [113–115], and by putting these data in relation to the functional networks identified by investigating the coherence of resting-state activity among nodes using either low-frequency blood oxygen level-dependent (BOLD) fluctuations (<1 Hz) or faster oscillations measured with MEG/EEG [116]. The general outcome of such studies is that nodes with strong anatomical connections also tend to exhibit enhanced coherence of resting-state activity (Box 4). Thus, in the visual domain, the functional networks that form and dissolve dynamically in a state- and goal-dependent way reflect well the architecture of coupling connections. Interestingly, as exemplified by the default network, the major hubs within the structural network are highly correlated with the major activation foci [117,118]. Developmental and longitudinal studies indicate that functional networks are susceptible to experience- and training-dependent modifications [119,120]. Thus, resting-state coherence shifts from predominantly interhemispheric to predominantly intrahemispheric during development [121] and networks identified by coherence in the beta-frequency range change from diffuse to focal, undergoing a transient phase of dramatically reduced coordination during late adolescence [122]. Coherence analysis of slow activity fluctuations also proved effective for the delineation of domain-specific default

Box 4. Resting-state networks

Resting-state fMRI allows one to examine the functional connectivity between brain regions independent of any task. Functional connectivity refers to inter-regional correlations of spontaneous brain activity. A consistent finding is that networks which tend to be correlated in their spontaneous activity during rest are similarly modulated by tasks involving the respective functional domains. At the group level, various networks and subnetworks have been reported (e.g., [136,137]). These networks include the motor network, the visual network, and two lateralized networks comprising superior parietal and superior frontal regions, as well as the so-called default network comprising the precuneus, medial frontal, and inferior parietal and temporal regions [138–140].

Besides the analysis of spontaneous brain activity during the resting state, a new line of research has been opened that characterizes more specific resting-state networks. It has been shown that domain-specific network information can be extracted from task-dependent fMRI data in a certain domain by removing specific experimental stimulation using low-frequency filtering that removes stimulus-locked correlations [141]. This method has recently been used to identify a so-called default language network that comprises those language-related brain regions known from functional language studies [123].

Box 5. Outstanding questions

- What are the general mechanisms that bring about network oscillations?
- What are the putative functions of oscillations and synchrony in different frequency ranges?
- Can nested oscillations provide evidence for parallel semantic and syntactic processes in the language network or their interaction and integration?
- How can neuronal networks encode, store, and replay information about sequences in general? Possible solutions to this problem have been proposed recently but are based on different concepts. One exploits the nonlinear dynamics of recurrent networks and is addressed as 'reservoir or liquid or echostate computing' [14]. The other uses 'deep learning' strategies in multilayered feedforward networks [142]. The question, however, remains how such strategies are implemented in the brain.

networks. Within the domain of language, this default network comprises major parts of the language-related brain regions, with a privileged coherence between those nodes (left BA 44 and pSTG) that constitute the sentence-processing system [123]. These are tightly linked by long-range white matter fiber bundles [124] and exhibit synchronization of activity in the theta-frequency band.

At a faster timescale, the spatiotemporal patterns of spontaneous activity closely resemble those occurring in response to sensory stimulation. This has led to the suggestion that spontaneous activity, by reflecting the genetically and epigenetically determined coupling architecture of networks, represents stored knowledge (priors) required for the processing and interpretation of sensory signals [125] (for a review see [14]) (Box 5).

Concluding remarks

At the neuronal level, complex cognitive processes appear to be implemented by the integration of a large number of local processes into multidimensional coherent global states or, in other words, by the hierarchical nesting of operations realized at different scales in densely interconnected subnetworks of variable size. These principles appear to hold for all cognitive subsystems, as illustrated in this review. Highly stereotyped, automatic processes such as syntactic computation are achieved in devoted subnetworks, as shown by the findings of strictly local processing of the most basic syntactic computations, whereas the more recent analyses of large-scale coherence reveal integration of these local processes into considerably wider and distributed networks. Processes that already rely on very large networks [88], such as semantic and interpretative processes, and that have to account for cultural and individual differences in meaning attribution are much more difficult to analyze as their nested dynamics are predictably more complex than those of the local networks devoted to elementary subprocesses.

Acknowledgment

This work was partly supported by a grant from the European Research Council (ERC-2010-AdG 20100407, NEUROSYNTAX, awarded to A.D.F.).

References

1 Broca, P. (1861) Remarques sur le siége de la faculté du langage articulé, suivies d‘une observation d'aphémie (parte de la parole). *Bull. Soc. Anat. (Paris)* 6, 330–357 (in French)
2 Wernicke, C. (1874) *Der Aphasische Symptomencomplex*, Springer Verlag (in German)
3 Hauser, M.D. *et al.* (2002) The faculty of language: what is it, who has it, and how did it evolve? *Science* 298, 1569–1579
4 Berwick, R.C. *et al.* (2013) Evolution, brain and the nature of language. *Trends Cogn. Sci.* 17, 89–98
5 Darwin, C.R. (1871) *The Descent of Man, and Selection in Relation to Sex*, D. Appleton
6 Deacon, T. (1997) *The Symbolic Species*, W.W. Norton
7 Fitch, W.T. (2010) *The Evolution of Language*, Cambridge University Press
8 Friederici, A.D. (2011) The brain basis of language processing: from structure to function. *Physiol. Rev.* 91, 1357–1392
9 Balaban, E. *et al.* (2010) Dynamic coordination in the brain – evolution of dynamic coordination. In *Dynamic Coordination in the Brain. From Neurons to Mind* (Von der Malsburg, C. *et al.*, eds), pp. 59–82, MIT Press and FIAS
10 Douglas, R.J. and Martin, K.A.C. (2004) Neuronal circuits of the neocortex. *Annu. Rev. Neurosci.* 27, 419–451
11 Markov, N.T. and Kennedy, H. (2013) The importance of being hierarchical. *Curr. Opin. Neurobiol.* 23, 187–194
12 Bullmore, E. and Sporns, O. (2009) Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat. Rev. Neurosci.* 10, 186–198
13 Sharma, J. *et al.* (2000) Induction of visual orientation modules in auditory cortex. *Nature* 404, 841–847
14 Singer, W. (2013) Cortical dynamics revisited. *Trends Cogn. Sci.* 17, 616–626
15 Emmorey, K. (2007) The psycholinguistics of signed and spoken languages: how biology affects processing. In *The Oxford Handbook of Psycholinguistics* (Gaskell, G., ed.), pp. 703–721, Oxford University Press
16 Fitch, W.T. and Hauser, M.D. (2004) Computational constraints on syntactic processing in a nonhuman primate. *Science* 303, 377–380
17 Gentner, T.Q. *et al.* (2006) Recursive syntactic pattern learning by songbirds. *Nature* 440, 1204–1207
18 Wilson, B. *et al.* (2013) Auditory artificial grammar learning in macaque and marmoset monkeys. *J. Neurosci.* 33, 18825–18835
19 Abe, K. and Watanabe, D. (2011) Songbirds possess the spontaneous ability to discriminate syntactic rules. *Nat. Neurosci.* 14, 1067–1074
20 Beckers, G.J.L. *et al.* (2012) Birdsong neurolinguistics: songbird context-free grammar claim is premature. *Neuroreport* 23, 139–145
21 Berwick, R.C. *et al.* (2012) A bird's eye view of human language evolution. *Front. Evol. Neurosci.* 4, 5
22 Petkov, C.I. and Jarvis, E. (2012) Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. *Front. Evol. Neurosci.* 4, 12
23 Chomsky, N. (2013) Problems of projection. *Lingua* 130, 33–49
24 Tankus, A. *et al.* (2012) Structured neuronal encoding and decoding of human speech features. *Nat. Commun.* 3, 1015
25 Mesgarani, N. *et al.* (2014) Phonetic feature encoding in human superior temporal gyrus. *Science* 343, 1006–1010
26 Quian Quiroga, R. *et al.* (2005) Invariant visual representation by single neurons in the human brain. *Nature* 435, 1102–1107
27 Hirabayashi, T. and Miyashita, Y. (2005) Dynamically modulated spike correlation in monkey inferior temporal cortex depending on the feature configuration within a whole object. *J. Neurosci.* 25, 10299–10307
28 Rabinovich, M. *et al.* (2008) Transient dynamics for neural processing. *Science* 321, 48–50
29 Gentner, T.Q. and Margoliash, D. (2003) Neuronal populations and single cells representing learned auditory objects. *Nature* 424, 669–674
30 Singer, W. (1999) Neuronal synchrony: a versatile code for the definition of relations? *Neuron* 24, 49–65
31 Churchland, M.M. *et al.* (2012) Neural population dynamics during reaching. *Nature* 487, 51–56
32 Georgopoulos, A.P. *et al.* (1986) Neuronal population coding of movement direction. *Science* 233, 1416–1419
33 Hubel, D.H. and Wiesel, T.N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* 160, 106–154
34 Recanzone, G.H. *et al.* (2000) Correlation between the activity of single auditory cortical neurons and sound-localization behavior in the macaque monkey. *J. Neurophysiol.* 83, 2723–2739

35 Mountcastle, V.B. (1957) Modality and topographic properties of single neurons of cat's somatic sensory cortex. *J. Neurophysiol.* 20, 408–434
36 Vinje, W.E. and Gallant, J.L. (2000) Sparse coding and decorrelation in primary visual cortex during natural vision. *Science* 287, 1273–1276
37 David, S.V. *et al.* (2004) Natural stimulus statistics alter the receptive field structure of V1 neurons. *J. Neurosci.* 24, 6991–7006
38 Buschman, T.J. *et al.* (2012) Synchronous oscillatory neural ensembles for rules in the prefrontal cortex. *Neuron* 76, 838–846
39 Olshausen, B.A. and Field, D.J. (2004) Sparse coding of sensory inputs. *Curr. Opin. Neurobiol.* 14, 481–487
40 Sajin, S.M. and Connine, C.M. (2014) Semantic richness: the role of semantic features in processing spoken words. *J. Mem. Lang.* 70, 13–35
41 Li, X. *et al.* (2006) Mental representation of verb meaning: behavioral and electrophysiological evidence. *J. Cogn. Neurosci.* 18, 1774–1787
42 Levelt, W.J.M. *et al.* (1991) The time course of lexical access in speech production – a study of picture naming. *Psychol. Rev.* 98, 122–142
43 Maess, B. *et al.* (2002) Semantic category interference in overt picture naming: sharpening current density localization by PCA. *J. Cogn. Neurosci.* 14, 455–462
44 Tyler, L.K. *et al.* (2004) Processing objects at different levels of specificity. *J. Cogn. Neurosci.* 16, 351–362
45 Halle, M. (1983) On distinctive features and their articulatory implementation. *Nat. Lang. Linguist. Theory* 1, 91–105
46 Pulvermüller, F. *et al.* (1999) Nouns and verbs in the intact brain: evidence from event-related potentials and high-frequency cortical responses. *Cereb. Cortex* 9, 497–506
47 Giraud, A.L. and Poeppel, D. (2012) Cortical oscillations and speech processing: emerging computational principles and operations. *Nat. Neurosci.* 15, 511–517
48 Waydo, S. *et al.* (2006) Sparse representation in the human medial temporal lobe. *J. Neurosci.* 26, 10232–10234
49 Gray, C.M. *et al.* (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature* 338, 334–337
50 Singer, W. (2009) Distributed processing and temporal codes in neuronal networks. *Cogn. Neurodyn.* 3, 189–196
51 Salazar, R.F. *et al.* (2012) Content-specific fronto-parietal synchronization during visual working memory. *Science* 338, 1097–1100
52 Buzsáki, G. *et al.* (2013) Scaling brain size, keeping timing: evolutionary preservation of brain rhythms. *Neuron* 80, 751–764
53 Steinmann, S.S. *et al.* (2014) Conscious auditory perception related to long-range synchrony of gamma oscillations. *Neuroimage* 100, 435–443
54 Nourski, K.V. *et al.* (2014) Functional organization of human auditory cortex: investigation of response latencies through direct recordings. *Neuroimage* 101, 598–609
55 Morillon, B. *et al.* (2010) Neurophysiological origin of human brain asymmetry for speech and language. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18688–18693
56 Bastiaansen, M.C.M. *et al.* (2005) Theta responses are involved in lexical–semantic retrieval during language processing. *J. Cogn. Neurosci.* 17, 530–541
57 Hagoort, P. *et al.* (2004) Integration of word meaning and world knowledge in language comprehension. *Science* 304, 438–441
58 Hald, L.A. *et al.* (2006) EEG theta and gamma responses to semantic violations in online sentence processing. *Brain Lang.* 96, 90–105
59 Penolazzi, B. *et al.* (2009) Gamma EEG activity induced by semantic violation during sentence reading. *Neurosci. Lett.* 465, 74–78
60 Obleser, J. and Kotz, S.A. (2011) Multiple brain signatures of integration in the comprehension of degraded speech. *Neuroimage* 55, 713–723
61 Mellem, M.S. *et al.* (2013) Gamma- and theta-band synchronization during semantic priming reflect local and long-range lexical–semantic networks. *Brain Lang.* 127, 440–451
62 Strauß, A. *et al.* (2014) Alpha and theta brain oscillations index dissociable processes in spoken word recognition. *Neuroimage* 97, 387–395
63 Sarnthein, J. *et al.* (1998) Synchronization between prefrontal and posterior association cortex during human working memory. *Proc. Natl. Acad. Sci. U.S.A.* 95, 7092–7096
64 Weiss, S. and Rappelsberger, P. (2000) Long-range EEG synchronization during word encoding correlates with successful memory performance. *Cogn. Brain Res.* 9, 299–312
65 Fell, J. *et al.* (2011) Medial temporal theta/alpha power enhancement precedes successful memory encoding: evidence based on intracranial EEG. *J. Neurosci.* 31, 5392–5397
66 Siapas, A.G. *et al.* (2005) Prefrontal phase locking to hippocampal theta oscillations. *Neuron* 46, 141–151
67 Sigurdsson, T. *et al.* (2010) Impaired hippocampal–prefrontal synchrony in a genetic mouse model of schizophrenia. *Nature* 464, 763–767
68 Sauseng, P. *et al.* (2005) Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *Int. J. Psychophysiol.* 57, 97–103
69 Summerfield, C. and Mangels, J.A. (2005) Coherent theta-band EEG activity predicts item–context binding during encoding. *Neuroimage* 24, 692–703
70 Roehm, D. *et al.* (2001) The role of theta and alpha oscillations for language comprehension in the human electroencephalogram. *Neurosci. Lett.* 310, 137–140
71 Weiss, S. and Mueller, H.M. (2003) The contribution of EEG coherence to the investigation of language. *Brain Lang.* 85, 325–343
72 Weiss, S. *et al.* (2005) Increased neuronal communication accompanying sentence comprehension. *Int. J. Psychophysiol.* 57, 129–141
73 Bastiaansen, M. *et al.* (2010) Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. *J. Cogn. Neurosci.* 22, 1333–1347
74 de Diego-Balaguer, R. *et al.* (2011) Brain dynamics sustaining rapid rule extraction from speech. *J. Cogn. Neurosci.* 23, 3105–3120
75 Meyer, L. *et al.* (2013) Left parietal alpha enhancement during working memory-intensive sentence processing. *Cortex* 49, 711–721
76 Meyer, L. *et al.* (2012) Spatiotemporal dynamics of argument retrieval and reordering: an fMRI and EEG study on sentence processing. *Front. Psychol.* 3, 523
77 Canolty, R.T. *et al.* (2006) High gamma power is phase-locked to theta oscillations in human neocortex. *Science* 313, 1626–1628
78 Aru, J. *et al.* (2015) Untangling cross-frequency coupling in neuroscience. *Curr. Opin. Neurobiol.* 31, 51–61
79 Johnsrude, I.S. *et al.* (2002) Functional imaging of the auditory system: the use of positron emission tomography. *Audiol. Neurootol.* 7, 251–276
80 Mummery, C.J. *et al.* (1999) Functional neuroimaging of speech perception in six normal and two aphasic subjects. *J. Acoust. Soc. Am.* 106, 449–457
81 Binder, J.R. *et al.* (2000) Human temporal lobe activation by speech and nonspeech sounds. *Cereb. Cortex* 10, 512–528
82 Hickok, G. and Poeppel, D. (2007) The cortical organization of speech perception. *Nat. Rev. Neurosci.* 8, 393–402
83 Giraud, A.L. *et al.* (2007) Endogenous cortical rhythms determine cerebral specialization for speech perception and production. *Neuron* 56, 1127–1134
84 Meyer, M. *et al.* (2002) fMRI reveals brain regions mediating slow prosodic modulations in spoken sentences. *Hum. Brain Mapp.* 17, 73–88
85 Friederici, A.D. and Alter, K. (2004) Lateralization of auditory language functions: a dynamic dual pathway model. *Brain Lang.* 89, 267–276
86 Patterson, K. *et al.* (2007) Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8, 976–987
87 Damasio, H. *et al.* (2004) Neural systems behind word and concept retrieval. *Cognition* 92, 179–229
88 Binder, J.R. *et al.* (2009) Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796
89 Vigneau, M. *et al.* (2006) Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *Neuroimage* 30, 1414–1432
90 Visser, M. *et al.* (2009) Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *J. Cogn. Neurosci.* 22, 1083–1094
91 Obleser, J. *et al.* (2007) Functional integration across brain regions improves speech perception under adverse listening conditions. *J. Neurosci.* 27, 2283–2289
92 Bornkessel, I. *et al.* (2005) Who did what to whom? The neural basis of argument hierarchies during language comprehension. *Neuroimage* 26, 221–233

93 Thompson-Schill, S.L. *et al.* (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc. Natl. Acad. Sci. U.S.A.* 94, 14792–14797

94 Fiez, J.A. (1997) Phonology, semantics, and the role of the left inferior prefrontal cortex. *Hum. Brain Mapp.* 5, 79–83

95 Friederici, A.D. and Gierhan, S.M.E. (2013) The language network. *Curr. Opin. Neurobiol.* 23, 250–254

96 Petersen, S. and Singer, W. (2013) Macrocircuits. *Curr. Opin. Neurobiol.* 23, 159–161

97 Chomsky, N. (1980) On binding. *Linguist. Inq.* 11, 1–46

98 Zaccarella, E. and Friederici, A.D. (2015) Reflections of word processing in the insular cortex: a sub-regional parcellation based functional assessment. *Brain Lang.* 142, 1–7

99 Grodzinsky, Y. and Friederici, A.D. (2006) Neuroimaging of syntax and syntactic processing. *Curr. Opin. Neurobiol.* 16, 240–246

100 Makuuchi, M. *et al.* (2009) Segregating the core computational faculty of human language from working memory. *Proc. Natl. Acad. Sci. U.S.A.* 106, 8362–8367

101 Meyer, M. *et al.* (2005) Distinct fMRI responses to laughter, speech, and sounds along the human peri-sylvian cortex. *Cogn. Brain Res.* 24, 291–306

102 den Ouden, D-B. *et al.* (2012) Network modulation during complex syntactic processing. *Neuroimage* 59, 815–823

103 Makuuchi, M. and Friederici, A.D. (2013) Hierarchical functional connectivity between the core language system and the working memory system. *Cortex* 49, 2416–2423

104 Skeide, M. *et al.* (2015) Brain functional and structural predictors of language performance. *Cereb. Cortex* Published online March 13, 2015. http://dx.doi.org/10.1093/cercor/bhv042

105 Hickok, G. and Poeppel, D. (2004) Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition* 92, 67–99

106 Rauschecker, J.P. and Scott, S.K. (2009) Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nat. Neurosci.* 12, 718–724

107 Bornkessel-Schlesewsky, I. *et al.* (2015) Neurobiological roots of language in primate audition: common computational properties. *Trends Cogn. Sci.* 19, 142–150

108 Ungerleider, L.G. and Mishkin, M. (1982) Two cortical visual systems. In *Analysis of Visual Behavior* (Ingle, D.J., ed.), pp. 564–586, MIT Press

109 Haxby, J.V. *et al.* (2001) Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293, 2425–2430

110 Tsao, D.Y. *et al.* (2003) Faces and objects in macaque cerebral cortex. *Nat. Neurosci.* 6, 989–995

111 Sporns, O. *et al.* (2002) Theoretical neuroanatomy and the connectivity of the cerebral cortex. *Behav. Brain Res.* 135, 69–74

112 Tononi, G. *et al.* (1998) Complexity and coherency: integrating information in the brain. *Trends Cogn. Sci.* 2, 474–484

113 Catani, M. *et al.* (2005) Perisylvian language networks of the human brain. *Ann. Neurol.* 57, 8–16

114 Kelly, C. *et al.* (2010) Broca's region: linking human brain functional connectivity data and non-human primate tracing anatomy studies. *Eur. J. Neurosci.* 32, 383–398

115 Thiebaut de Schotten, M. *et al.* (2012) Monkey to human comparative anatomy of the frontal lobe association tracts. *Cortex* 48, 82–96

116 Weisz, N. and Obleser, J. (2014) Synchronisation signatures in the listening brain: a perspective from non-invasive neuroelectrophysiology. *Hear. Res.* 307, 16–28

117 Deco, G. *et al.* (2011) Emerging concepts for the dynamical organization of resting-state activity in the brain. *Nat. Rev. Neurosci.* 12, 43–56

118 Deco, G. and Jirsa, V.K. (2012) Ongoing cortical activity at rest: criticality, multistability, and ghost attractors. *J. Neurosci.* 32, 3366–3375

119 Perani, D. *et al.* (2011) The neural language networks at birth. *Proc. Natl. Acad. Sci. U.S.A.* 108, 16056–16061

120 Taubert, M. *et al.* (2011) Long-term effects of motor training on resting-state networks and underlying brain structure. *Neuroimage* 57, 1492–1498

121 Fair, D.A. *et al.* (2007) Development of distinct control networks through segregation and integration. *Proc. Natl. Acad. Sci. U.S.A.* 104, 13507–13512

122 Uhlhaas, P.J. *et al.* (2009) The development of neural synchrony reflects late maturation and restructuring of functional networks in humans. *Proc. Natl. Acad. Sci. U.S.A.* 106, 9866–9871

123 Friederici, A.D. *et al.* (2011) Maturation of the language network: from inter- to intrahemispheric connectivities. *PLoS ONE* 6, e20726

124 Friederici, A.D. (2009) Pathways to language: fiber tracts in the human brain. *Trends Cogn. Sci.* 13, 175–181

125 Clark, A. (2013) Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* 36, 181–204

126 Friederici, A.D. *et al.* (2006) The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proc. Natl. Acad. Sci. U.S.A.* 103, 2458–2463

127 Sanides, F. (1962) Architectonics of the human frontal lobe of the brain. With a demonstration of the principles of its formation as a reflection of phylogenetic differentiation of the cerebral cortex. *Monogr. Gesamtgeb. Neurol. Psychiatr.* 98, 1–201

128 Amunts, K. and Zilles, K. (2012) Architecture and organizational principles of Broca's region. *Trends Cogn. Sci.* 16, 418–426

129 Bolhuis, J.J. *et al.* (2010) Twitter evolution: converging mechanisms in birdsong and human speech. *Nat. Rev. Neurosci.* 11, 747–759

130 Bierwisch, M. (1982) Formal and lexical semantics. *Linguist. Ber.* 80, 3–17

131 Collins, A.M. and Loftus, E.F. (1975) Spreading activation theory of semantic processing. *Physiol. Rev.* 82, 407–428

132 Miller, G.A. (1978) Semantic relations among words. In *Linguistic Theory and Psychological Reality* (Halle, M. *et al.*, eds), pp. 60–118, MIT Press

133 Jackendoff, R. (1983) *Semantics and Cognition*, MIT Press

134 Pustejovsky, J. (1995) *The Generative Lexicon*, MIT Press

135 Lakoff, G. (1987) *Women, Fire, and Dangerous Things. What Categories Reveal about the Mind*, University of Chicago Press

136 Beckmann, C.F. *et al.* (2005) Investigations into resting-state connectivity using independent component analysis. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 360, 1001–1013

137 Fox, M.D. and Raichle, M.E. (2007) Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nat. Rev. Neurosci.* 8, 700–711

138 Buckner, R.L. and Vincent, J.L. (2007) Unrest at rest: default activity and spontaneous network correlations. *Neuroimage* 37, 1091–1096

139 Raichle, M.E. and Snyder, A.Z. (2007) A default mode of brain function: a brief history of an evolving idea. *Neuroimage* 37, 1083–1090

140 Greicius, M.D. *et al.* (2008) Persistent default-mode network connectivity during light sedation. *Hum. Brain Mapp.* 29, 839–847

141 Lohmann, G. *et al.* (2010) Setting the frame: the human brain activates a basic low-frequency network for language processing. *Cereb. Cortex* 20, 1286–1292

142 Mnih, V. *et al.* (2014) Human-level control through deep reinforcement learning. *Nature* 518, 529–533