

REVIEW OF PAPER *GROUNDING LANGUAGE PROCESSING ON BASIC NEUROPHYSIOLOGICAL PRINCIPLES BY FRIEDERICI AND SINGER (2015)*

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ABSTRACT

In this didactic and information-packed article by Friederici and Singer (2015), entitled *Grounding language processing on basic neurophysiological principles*, the authors propose to investigate the generality of these principles. For this purpose language is the ultimate test case because if it proves to rely, in essence, on these basic neuronal mechanisms, as other cognitive systems have proven to do, it makes a pretty strong case. It would mean that even cognitive functions unique to the human species, such as language, are amenable to comparison not only to other cognitive functions within humans, but also to neuronal circuitry we find in other species. This would open up a host of new and exciting possibilities for research. In this paper, the authors offer a wide variety of empirical evidence for the dependence of language on distributed computations in specialized cortical areas forming large-scale dynamic networks. As such, their operating basics seem indeed similar to those in other cognitive functions as well as other species. In this review, I will first elaborate on their main argument, and subsequently, I will discuss each principle proposed and elaborate on examples presented by the authors, as well as contribute with new examples.

Some odd 15 years ago, David Poeppel, currently with the Max Planck Institute in Frankfurt, attempted to solve the enigma of pure word deafness (POEPEL, 2001). Patients who receive this diagnosis as a result from brain lesions, usually in the superior temporal gyrus, are unable to comprehend words, yet often they are quite capable of sublexical tasks such as counting syllables. They also succeed in auditorily distinguishing between basic acoustic differences, such as in frequency discrimination task. Surprisingly, this does not help their poor performance on phoneme level distinction. And even though they present major perception deficits, they generally have no problem speaking, reading, and writing. Furthermore, the degree in which they vary in terms of sublexical capacities largely correlates to the anatomical location of their lesions (mainly whether they are left lateralized or bilateral). From this, the author concludes that different functions must underlie three different, but often mistaken, tasks: (i) auditory perception (perceiving acoustic differences and segregating speech sounds from non-speech sounds), (ii) speech perception (involving sublexical elements), and (iii) speech recognition

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(mapping sound to lexical representations). In particular, he concludes that parallel streams must serve speech perception, in which left lateralized structures are involved in phoneme level processing, whereas right lateralized structures carry out syllable level processing.

In his paper, Poeppel was able to ground his claims on basic neurophysiological computational principles. One of them being that ensembles of neurons responsible for executing specific tasks (such as the processing of acoustic phonetic features) synchronize their firing patterns, such that they operate in union producing oscillatory patterns that fall within specific frequency bands. It appears that left lateralized neuronal populations preferably oscillate in fast gamma band frequencies (~40Hz), whereas right lateralized neuronal populations prefer slower theta frequency bands (in fact, theta (4–8 Hz) and delta (1–3 Hz)). The respective parsing frequencies of these neuronal oscillating ensembles seem to converge on the specific short and longer time windows of phonemes and syllables, respectively. These are processed in parallel streams, the outcomes of which are to be consequently integrated. The fact that these ‘micro tasks’ are distributed in a parallel fashion, and thus can occur concomitantly in laterally specialized areas, adequately accounts for the eclectic and often counter intuitive abilities of patients with word deafness, as well as patterns of other language deficits.

This initial model later on culminated in the now seminal article of Hickok and Poeppel in 2007, *The cortical organization of speech processing*. It was in that paper that the authors formalized their dual stream network for speech processing, hosting the aforementioned parallel bilateral ventral¹ streams, responsible for processing speech signals for comprehension, and a left-lateralized dorsal stream, responsible for mapping acoustic speech signals onto motor articulatory networks. Dual-stream models such as these are also present in non-language domains, such as the visual system (HICKOK & POEPEL, 2007; FRIEDERICI, 2011; BERWICKE *et al.*, 2013). Moreover, the organization of cognitive systems into distributed networks, where functions are distributed over local circuits connected by fiber tracts² over longer distances, is ubiquitous not only across various cognitive systems within humans, but also across different species. Non-human primates, for instance, share our make-up of the visual dual stream system, boasting similar intrinsic organizational properties: i.e. dorsal streams grasp movement, while ventral streams encode other visual features. These streams are optimized through experience-dependent pruning of connections and learning dependent enhancement. The fact that they are similar for non-human primates and humans, given particularities of experience for each of the species, indicates a shared genetic determination of wiring patterns.

This is where we get to the main point Friederici and Singer are trying to make in the paper presently under review: *Grounding language processing on basic neurophysiological principles*. Irrespective of cognition specificity or even species, similar basic neurophysiological principles are at work, based on the fact that cortical neurons display the same biophysical properties across cognitive systems as well as species. And much the same goes for the organization of excitatory and inhibitory subtypes of neurons, and manner in which cortical areas are connected. This fact is of great relevance to the

1. In anatomy, ventral refers to the anterior or inferior side of an anatomical structure, while dorsal refers to the superior or posterior side of an anatomical structure. Ventral and dorsal are associated to the belly and back as anatomical coordinate references (BEAR *et al.*, 2002)

2. Fiber tracts are composed of threadlike extensions of nerve cell axons, which generally serve to connect brain areas over longer distances. They can be visualized by way of diffusion MRI (or dMRI), which is a magnetic resonance imaging (MRI) method which by capturing the diffusion process of, mainly, water molecules, which are present in all biological tissues.

further understanding of language processing in the brain, Friederici and Singer argue, especially in light of the limitations of non-invasive research methods, such as Electroencephalography (EEG), Magnetoencephalography (MEG) and Functional Magnetic Resonance Imaging (fMRI)³.

These techniques, which have developed over the past 40 years, have yielded enormous contributions to the mapping of the functional anatomy of language processing; however, the vast majority of these measures occur outside of the skull. That is, enlightening as the resulting data are, they only offer indirect evidence of neurophysiological activity, and as such cannot account for underlying processes at cellular and micro circuit level.

Direct evidence of neuronal ensemble activity, through intracranial measures are rare in humans, solely performed on patient groups. Highly invasive techniques, such as multi-array electrode implants are performed during procedures that require surgical intervention anyway, such as pre-operative clinical assessment or neurosurgery. Such is the case of the study on phonetic feature representation by Mesgarani *et al.* (2014), where intracranial measures on the cortical surface of the super temporal gyrus (see Figure 1) were acquired in six epileptic patients. Animal models allow for more elaborate intracranial measures. Nevertheless, investigations into language processing by way of animal models can only take us so far, as extensive research shows that core linguistic functions, such as syntax, are exclusive to the human species (BERWICKE *et al.*, 2013, FREDERICI, 2011). On the other hand, basic neurophysiological principles, such as neuron cell structure, excitatory and inhibitory processes, and intercellular communications are largely comparable among species. In fact, it is largely through studies on animals that neuroscientists know as much as they do (BEAR *et al.*, 2002). It is these basic neuronal structures and operations that are ultimately responsible for the storage of information, and determine the computational algorithms that process input and relay output between local and long distance brain circuits.

Friederici and Singer are of course not the first to advocate for the understanding of neurophysiological computational principles as critical for the advancement in the field of the neuroscience of language. Other researchers, such as Poeppel, Indefrey, Hagoort and Hickok have all argued the same case (POEPEL, *et al.*, 2012; INDEFREY, 2011; HAGOORT, 2005; HICKOK, 2012). However, the paper under review has an explicit didactic objective, as well as providing a broad overview of recent findings in the literature that underscore the applicability of neurophysiological principles in resolving long-standing questions about the neuronal architecture of language processing. Thus, the authors argue for language as a test case for the explanatory power of these principles:

“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.” (FRIEDERICI & SINGER, 2015; p. 1)

3. Electroencephalography (EEG) and Magnetoencephalography (MEG) record electrical activity of the brain along the scalp. EEG measures voltage fluctuations as a result of ionic current caused by intricate electrochemical interaction between neurons. MEG measures the magnetic fields produced by these electrical currents, using very sensitive magnetometers. Functional magnetic resonance imaging (fMRI) detects changes in blood flow. This supposedly correlated with neuronal activity, as it restocks neurons with nutrition (especially oxygen) after having depleted resources due to previous activity (BEAR *et al.*, 2002)

Generality here is not to be mistaken for the generality of cognitive functions, but rather it reflects the idea that all cognitive functions - no matter how specific or complex - can ultimately be reduced to basic neurophysiological mechanisms that are common to all of them.

Having laid out the initial arguments of their proposal, the authors then proceed to present sections each elaborating on a given principle, going from micro to macro level, illustrated by various examples from recent studies in the literature. In my review, I have explicitly transformed the section headers into principle definitions, which results from my interpretation of the flow of their ideas, and does not follow directly from the article. I also explain and comment on some of the examples brought up by the author, as well as add new examples from the literature not cited by Friederici and Singer themselves. For visual reference to the brain areas described in this paper, I refer to Figure 1, as a general guideline.

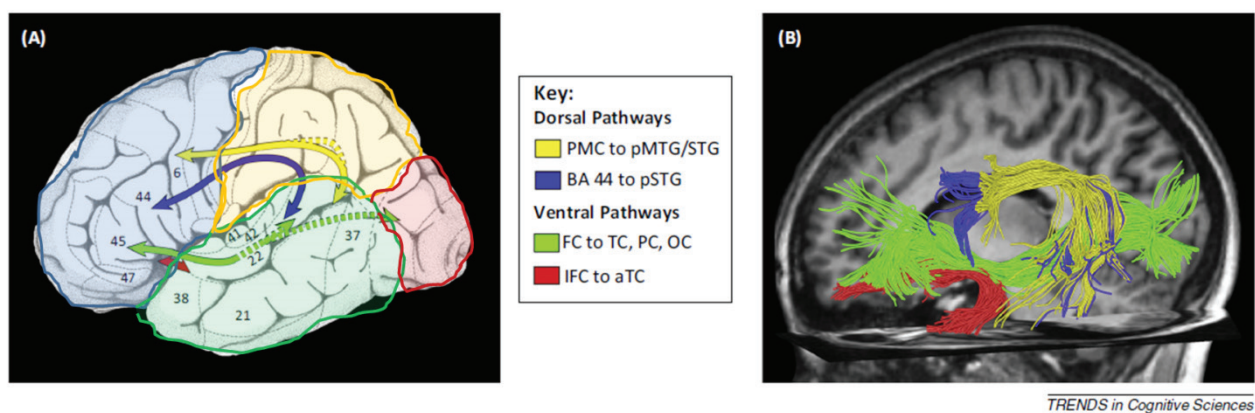


Figure 1: Adapted from *Grounding language processing on basic neurophysiological principles* (FRIEDERICI & SINGER, 2015). A: a schematic visualization of fiber tracts (the arrows), and a rough indication of anatomic division of brain areas: frontal lobe (blue), temporal lobe (green), parietal lobe (yellow) and occipital lobe (red). The brain is viewed from the left hemisphere. Indications such as anterior and posterior refer to horizontal orientations (in direction of the nose and back, respectively) within the respective lobes, while superior and inferior indicate vertical positions. B: visualization of fiber tracts on the left hemisphere as a product of Diffusion Tensor Imaging.

Principle 1: There is a 'canonical' microcircuit according to which locally connected neurons operate across cognitive systems or species.

This principle refers to the idea that it is mainly the manner in which systems are organized that determines their specificity. Evidence for this emphasis on the organization of microcircuits (locally connected neuronal ensembles) as opposed to there being any specificity to the neurons themselves at an individual level, is represented in the concept of the pluripotency of neural cells. An example is the well-known phenomenon of enhanced visual abilities in early deaf people. How this reflects in the cortical organization was studied intracranially in congenitally deaf cats compensating for their deficit by using part of their auditory cortex for extensive visual processing absent in hearing cats (LOMBER, 2010). In another study on ferrets, the authors discovered that if thalamic projections are rerouted to the auditory cortex, such that visual input during acquisition is processed in auditory cortex, visual maps are formed there (SHARMA *et al.*, 2000).

The key element to these results is that, even though visual maps are formed in the auditory cortex, the sensory processing modules that arise there acquire comparable organization to those in the visual cortex (i.e. groups of cells only respond to preferred orientation of visual objects, while others respond to movement).

What is then canonical about these microcircuits is the way in which these microcircuits connect, anatomically via an intricate web of axioms and dendrites, and operationally via a complex interaction between excitatory and inhibitory feedback among connected neurons that orchestrates small neuronal ensembles to activate in synchrony. It is through the nature of input that these microcircuits self-organize into highly specialized functional assemblies, in which the association between connected neurons may further strengthen or weaken when learning alters the weights of connections. That is, functional specificity lies not in the intrinsic specialization of the individual neurons nor do fundamental neurophysiological principles that mediate information exchange between them vary. Neurons *become* specialized through the manner in which they are connected to other subcortical and cortical areas, and the input they thus receive, and the output they pass on to other functional neuronal groups that makes for functional specificity. It is how neurons are embedded within anatomical structure a circuit which ultimately confers a high degree of specialization to a given microcircuit.

Principle 2: it is the particular temporary configurations of cooperating neurons in distributed micro networks tuned to specific features that encode neuronal representations rather than individual specialized neurons

At this point, Friederici and Singer cite an example as a reference, but do not elaborate on it. As it illustrates the principle well, I would like to treat this intriguing study by Mesgarani *et al.* (2014) in greater detail. The authors investigated the neural representation of phonemes in the left superior temporal gyrus using intracranial recordings of an implanted multi-array of electrodes in a small group of epileptic patients (with no language deficit). These electrode arrays allow for the direct measurement of stimuli-selective responses of small neuronal ensembles. What the data showed very clearly is that neurons do not respond selectively to phonemes, but rather are tuned to specific acoustic-phonetic features, such as those that characterize phonetic natural classes (e.g. obstruent vs. sonorant). Phonemes are thus neurally represented by a given combination of activated neurons, and a given neuron within that combination can participate in more than one small scale distributed network, i.e. each network representing a specific combination of phonetic features.

These small scale distributed networks are ubiquitous across a variety of sensory systems (visual, olfactory), which makes it feasible to test such networks in animal models. Moreover, it presents a plausible account for the combinatory and transient nature of language (for combinations of constituents are not fixed, but infinite and unpredictable). That is, we might imagine feature selective neurons to flexibly recombine to form phoneme combinations, which in turn, form infinite number of words, combination of words into infinite number of phrases and sentences, etc.

This kind of organization supposes some kind of hierarchical structure, in which small scale networks are integrated with other assemblies of neurons that oscillate at a spatial distance at different

frequencies, forming macro-structures of feature responsive assemblies. This obviously adds to the enormous complexity of signals which challenging if not nearly impossible to analyze with the techniques currently available.

Principle 3: sparse coding

This principle emphasizes the fact that representations stored in long term memory seem to be encoded by only a limited (hence, sparse) number of highly specialized neurons and are activated during a limited timeframe. Here, Friederici and Singer focus on semantic coding, specifically in the medial temporal lobe, presenting evidence from intracranial recordings responses to both celebrity's faces and names, indicative of abstract amodal semantic representations. However, in convergence with data from several lexical studies, there is a strong indication that the specific response is in fact to a semantic category, or a feature, rather than to the semantic item itself. Evidence comes from behavioral results and indirect neurophysiological recording. The first type of data shows that lexical representations that are rich in features speed up processing in comparison to items with fewer, more generic semantic features (i.e. *lemon* (acidic, yellow, oval, etc.) vs. *fruit*), especially when random auditory background noise enhances the role of semantics for achieving recognition (SAIJN & CONNINE, 2014). Neurophysiological results also show feature effects when prime and target words, like *tiger* and *lion*, are presented at short intervals, in which case there is facilitation of access of *lion* after *tiger*. However, when similar pairs are presented at longer intervals, interference of access is brought about. This is probably due to the activation history of individual cells representing a particular feature that may participate in overlapping ensembles (*tiger* and *lion* are both felines, for example), as once activation is brought down again after recognition, extra cognitive effort is needed to reactivate (LEVELT *et al.*, 1991). The feature account of semantic coding is especially advantageous for lexical representation as it is preferable to have a certain degree of underspecification of semantic features for a lexical item given that structural and discourse context may greatly influence and complete semantic interpretation of words.

As with principle 2, we might expect sparsely coded representations to bind other sparsely coded representations forming macro structures. Such that, phoneme-specific assemblies bind with word-specific assemblies, to be bound with semantic connotations (extra linguistic representations, such as motor representation for verbs, or visual sensory representations for easily visualized nouns); these combined assemblies will then become the units for larger assemblies (activated over a longer period of time) bound together by syntactic rules and operations (such as merge). These meta-assemblies would lead to the buildup of transient syntactic and semantic structures.

We may imagine this binding together, also known as hierarchic nesting, to be managed by the synchronization of distinct local oscillatory patterns (such as Hickok and Poeppel suggest for speech recognition). But it is difficult to falsify these hypotheses at higher, extremely complex levels, if not due to complex interactions between assemblies, by the sheer number of neurons in activation – a hardly sparse estimated 2 million neurons for a given percept in the medial temporal lobe (FRIEDERICI & SINGER, 2015). The further development of this issue brings us to principle number 3.

Principle 3: assemblies of temporarily bound neurons are marked by coherence of oscillatory activity

Friedrici and Singer do not go into the biological underpinnings of oscillatory patterns, but it might be useful to explain, even if not in depth, some of the basics here. Generally the oscillatory patterns recorded from neuronal ensembles reflect synchronized electrochemical activity of many neurons. Ever changing voltage potential which give rise to sinuous measures are the results of changing polarities in and around post-synaptic areas where the many dendrites of, mostly pyramid cells in the outer layers of the cortex, meet axons of other cells. It is there where we can find the reflections of interneuronal communication, either through excitatory or inhibitory feedback between connected neuron cells. Oscillatory rhythms are thus the results of synchronization of such activity of many cells. This synchronization may be brought about by different mechanisms, that is, connected neurons may adjust to each other's rhythms by interneuronal feedback, or alternatively, one pace maker type of neuronal structure takes on the 'director' role of regulating rhythms (BEAR *et al*, 2002). Neuronal microcircuits are thus characterized by attaining synchronized neuronal activities, and the nature of their activity may be reflected by the specific frequency band they oscillate at. The main four frequency bands established for neuronal activity are alpha, beta, delta, theta and gamma.

For speech processing, reaffirming claims from the dual stream model for speech processing presented in 2007, Giraud and Poeppel (2012) explain the relation between frequency bands and linguistic functions as such:

(...) the low gamma (25–35 Hz), theta (4–8 Hz) and delta (1–3 Hz) bands provide a link between neurophysiology, neural computation, acoustics and psycholinguistics. The close correspondences between (sub)phonemic, syllabic and phrasal processing, on the one side, and gamma, theta and delta oscillations, on the other, suggest potential mechanisms for how the brain deals with the 'temporal administrivia' that underpin speech perception. (GIRAUD & POEPEL, p. 511)

As to how these function specific rhythms are integrated, there are hypotheses involving phase–amplitude cross frequency coupling, which means that the phase of the low frequency component modulates the amplitude of the high frequency activity varying with along with this concomitant slow rhythm, thus binding information processed at different sampling speeds (ARU *et al.*, 2015). It is part of the very nature of brain activity that oscillations of different frequencies coexist and exhibit this phase–amplitude coupling.

With regard to the content of the representations, lower frequencies are associated to superordinate content (e.g. overarching categories), while fast oscillating rhythms encode more specified items, and coupling mechanisms may thus bind these.

Principle 4: frequency range is characteristic for the spatial distance of the extensions of the assemblies

Another correlation that is suggested by Friederici and Singer is that between frequency bands and topographic distance. Thus, spatially restricted processes would be characterized by rapid gamma frequency, whereas synchronization in lower frequency bands, such as beta, and theta, characterizes

spatially extended processes. Seemingly, a similar correlation also holds for less vs. more number of neurons, which may present a possible confound, as usually spatially extensive networks also engage a larger number of neurons.

Here Friederici and Singer suggest that linguistic tasks involving memory recall and extensive networks (widely distributed networks) both due to the integration of different levels of information, supposedly engage bigger neuronal population responses, which are also spatially more distributed. Thus, they are typically coordinated in theta and beta frequency band. In order to support this claim, the authors offer evidence from EEG measures. Then, they correlate gamma band intensity increase with semantic violations task. In fact, this would be unexpected given the previously presented hypothesis that slower frequencies are associated to operations requiring extensive networks. Let us observe the semantic violations as present in the stimuli of the cited study (HALD *et al.*, 2006), which are as follows: *Dutch trains are white/sour* (in contrast to expected *yellow*). Violation resolution hinges on integration of world knowledge (outside of the language domain), i.e. Dutch trains are in fact yellow, and trains cannot be sour tasting. In sum, an integration over wide spread networks is to be expected associated with slower theta and beta frequencies, and not faster gamma oscillations. And indeed, what Hald *et al.* (2006) find is theta band increase for semantic violation vs. gamma band increase for correct sentences (which suggest they are more locally processed).

Nonetheless, Hald *et al.* (2006) caution the reader that theta increase may not necessarily be due to semantic processing *per se* (integrating semantic info) but with extended tasks, such as error detection, memory load increase, etc. This is still consistent with Friederici and Singer's overall hypothesis, but may not be relevant to language processing itself but rather to the specific context of experimental conditions. A similar problem exists for experiments focusing on syntactic processing. Typically, this variable is manipulated by increasing syntactic complexity (e.g. by increasing distance in between syntactic dependencies), such that there is usually an added complexity due to memory load, which is associated to alpha enhancement.

Furthermore, in interpreting evidence offered by Friederici and Singer, we must keep in mind that oscillation measures in healthy humans are calculated from neurophysiological signals that were recorded extracranially. Frequency band analyses, the result of calculations done by mathematic models, are thus applied on signals that are much noisier due to the fact that electrodes are placed at a distance from generator sources, with biological matter as obstacles. In fact, it is not to be taken for granted that such analyses are able to determine the pure source and make up of these signals.

Principle 5: Different scales of networks require different measures

For small scale networks, local field potentials are measured to reveal patterns of activation either intra- or extracranially (the latter with EEG or MEG). The power of these signals increase by two factors: (i) with large numbers of neurons participating in a synchronous assembly or (ii) with the precision of synchronization. In the first case, large numbers give rise to extremely regular wave patterns with lower amplitudes, usually characterized alpha band frequencies. These patterns may represent resting states, and are usually not very functionally specific. The second case, in which

small numbers of neurons oscillate with great synchronous precision, noisy wave pattern arise, but within this complexity, there is great intensity (in amplitude) for given frequency bands. It is this latter case that characterizes, for instance, ERP (Event-Related Potentials)⁴ components, such as the N400, a typical neurophysiological signature for syntactic-semantic processing. ERPs are wave patterns to which various frequencies contribute, and they have been associated to increase in delta (1-4Hz) and gamma frequency, mostly, and less so to theta frequencies (RHOEM *et al.*, 2007).

Large scale networks that connect local circuits across cortical areas are mapped by looking at coherence of oscillatory signals. Coherence measures can be analyzed by multiple perspectives: (i) functional connectivity, in which statistical analysis is done on large scale activation patterns to see if there are statistically relevant correlations; (ii) direct causal relations, where one pattern of activity consistently follows the other: (iii) and structural anatomical connections.

Of the second type of coherence, there is an interesting study by Acheson and Hagoort (2013), not cited by Friederici and Singer, but which illustrates a different approach to coherence analysis. This study investigates the causal relation between lexical level and syntax level processes, which are thought to be served by middle temporal gyrus (MTG) and inferior frontal gyrus (IFG) (location of Broca's area), respectively. Most models of language processing assume a canonical order of causal (temporal) relation between domains (i.e. from phonemes to lexicon to syntax). However, in terms of connectivity this is not to be taken for granted. In this study, transcranial magnetic stimulation (TMS)⁵ is used to temporarily interrupt processing locally. They used stimuli in Dutch with temporal ambiguity due to lexical ambiguity (the word can be either a noun or verb), with sentences that literally translate as *You can bake/box and baskets buy at the market*⁶. The ambiguity is brought up by the word *bakken*, which in Dutch can mean both *to bake* or *boxes*. The resolution of the ambiguity can occur when the words *baskets* is read, which leads to the nominal reading of *bakken*. (i.e. as *boxes*). Both for TMS and IFG regions there is a delay for reading ambiguous sentence regions (*bakken*) when TMS emission occurs concomitantly; however, for the disambiguating sentence region (*baskets*), there is a delay, specifically when TMS exposure is focused on IFG (as compared to similar exposure for control sentences). This shows that IFG has a clear causal connection in which lexical items that are activated are subsequently integrated into larger scale syntactic structures.

The third coherence factor, which is related to the anatomical realization of the brain connectome, is high on the agenda of Friederici's research team (FRIEDERICI, 2011; BERWICK *et al.*, 2013). It forms the basis for her dual stream language processing model, presented in the next section.

4. "Event Related brain Potentials are measures extracted from continuous EEG recordings in which stimulus presentation onset is coupled in time with brain responses so that the neurophysiological responses can be robustly related to stimuli. Segments are added and averaged per experimental condition so that they may be compared for condition effects. This is measured by comparing amplitudes (in voltage) and latencies (moment of maximum peak in ms) in a given time interval." (SOTO *et al.*, 2015)

5. During a Transcranial Magnetic Stimulation (TMS) procedure, a magnetic field generator, in the shape of a small circular coil is placed near the head of the person. This coil provides small electric currents by way of electromagnetic induction. There is high precision in the localization of the currents, and may cause excitatory or inhibitory action on the neurons in the region it is applied to.

6. The original sentence: *Je kunt bakken(N/V) en manden kopen op de markt*, which translates roughly to *You can buy boxes/bake and baskets at the market* (ACHESON & HAGOORT, 2013)

Principle 6: Anatomical maturity of connection between cortical areas can correlate to developmental processes

Friederici and Singer here briefly present an outline of Friederici's dual stream model, which maps out connections between areas in the left temporal lobe and inferior frontal gyrus, canonically associated to language functions at lexical and syntactic level, respectfully. Two main processing streams are proposed: (i) a ventral stream in which middle and anterior temporal lobe regions are connected to the inferior frontal gyrus by ventrally located fiber tracts (the uncinate fasciculus and the extreme capsule fiber system) and (ii) a dorsal stream connecting the inferior frontal gyrus (BA 44) to the posterior temporal gyrus, partly running through a dorsal fiber tract, named the arcuate fasciculus and superior longitudinal fascicle (see Figure 1) (FRIEDERICI, 2012; BERWICK *et al.*, 2013).

Strikingly, in contrast to the ventral fiber tracts, the dorsal tracts are subject to slow maturation during infancy. They connect areas with high statistical coherence patterns for processing of syntactic complexity, and the maturation of the fiber tracts that bind them correlates with the increasing ability of children regarding the processing of verbal memory demanding, syntactically complex sentences as a result of language acquisition. On the other hand, in non-primates, these dorsal tracts are also present, as well as the ventral streams, but contrary to what happens with children, dorsal tracts remain structurally weak in these animals throughout their lifespan (BERWICKE *et al.*, 2013)

Importantly, Friederici and Singer conclude, the proposal of such a relatively widespread functional network is warranted based on other similarly structured cognitive networks (for processing polymodal sensory objects and control of attention, for instance), which show that "anatomical connections form the 'backbone' of networks over which connections are enhanced by coherence of temporally structured activity" (FRIEDERICI & SINGER, 2015).

Principle 7: There is an ideal configuration of connectivity

Apparently the ideal level of connectivity that can deal with the highest degree of complexity in a system, is when interconnected hubs are somewhere in between complete regularity (such as the edges of crystal atoms) and totally randomly formed connections. Neuronal networks as mediated by synaptic connections and activation weights determined by learning processes (which alter feedback dynamics between neurons), represent these ideal connectivity values. Within cognitive anatomical architecture, there are strategic hubs that serve the highest most complex cognitive function. One methodology of visualizing these optimal networks is by resting state fMRI recordings. The idea behind resting state networks is that spontaneous brain activity can be measured while subjects are not engaged in a specific task, but theoretically in a 'resting'. It is often so that spontaneous activity reveals functional networks even when subjects are not engaging in any specific cognitive function because these networks always present extreme high connectivity values as measured by coherence of oscillatory patterns. For language, there is a privileged connectivity between the inferior frontal gyrus, more specifically region BA44, and the posterior superior temporal gyrus. This connectivity is structured on anatomical connections in the form of large fiber bundles (the arcuate fasciculus) and is reflected by coherent oscillations in the theta band in the connected areas. The fact that sensory

processing within that same region occurs at faster gamma frequencies strengthens the hypothesis that information is integrated by coupling co-occurring slow and faster frequencies as described in previous sections.

In conclusion, we may say that if language is a test case for the explanatory power, based on the wealth of information contained in Friederici and Singer's paper, they have succeeded in their quest. Also, it is not a coincidence that we see the prolific publication of papers with similar tenets, as mentioned earlier in this review (POEPPPEL, *et al.*, 2012; INDEFREY, 2011; HAGOORT, 2005; HICKOK, 2012). It is true that the more evident success stories have been achieved in domains that are reasonably low level, and for which variables are easier to tease apart, such as for the representation and processing of sublexical levels. However, if we take the basic thesis of this article to be true, we must conclude that (i) microcircuits with their general configurational and operational properties are at the base of any cognitive system, whether within or outside of the domain of language; (ii) evidence from computational principles from domains other than language are just as relevant to the understanding of language processing; (iii) by extension, evidence for computational principles from animal models are indeed informative to the understanding of language processing.

On a more general note, we may surely conclude that functionality should be seen in a distributed and connective model. For the neuroscience of language, this entails what Poeppel described as "the well-deserved retirement of the classical brain-language model" (POEPPPEL *et al.*, 2012). The long-standing notion of fixed anatomical areas as reflecting "production" or "perception" of language is obviously mistaken. And even now we have reached a more detailed granularity of linguistic function, we must still be wary of associations between functions and regions. There is probably not one region responsible for lexical level processes, for example, but rather many distributed microfunctional networks that depend on coherence dynamics to carry out such tasks.

As if the highly complex technicality of the workings of neuronal computation and neuronal biology was not complex enough, due to advancements in compatibility between linguistics and neuroscience, the diversity of linguistic theories is also seeping in. There are now studies testing hypotheses based on a variety of competing theoretical frameworks, ranging from cognitive grammar to micro-derivational theories (ALLEN *et al.*, 2012; PYLKKANEN, L., BRENNAN, J.; BEMIS, D. K., 2010). This of course can only add to the richness of the data, but is a fact mostly overlooked by papers in neuroscience, as they tend to presuppose a homogenous view of the domains of language by linguists. In part this stems from a, to a certain degree, healthy detachment from theory, but it is also a testament to recent breakthroughs that this homogeneity is not broken down, seeing that the field has matured up to a point where more detailed and profound questions can be asked. I would agree with Friederici and Singer that the coming of age of the neuroscience of language is largely due to the shifted focus from mere anatomical localization to anatomical organization as foreseen by neurophysiological computational principles, which makes this soon to be seminal paper by Friederici and Singer a must-read.

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