Introduction

Towards a new functional anatomy of language

Abstract

The classical brain-language model derived from the work of Broca, Wernicke, Lichtheim, Geschwind, and others has been useful as a heuristic model that stimulates research and as a clinical model that guides diagnosis. However, it is now uncontroversial that the classical model is (i) empirically wrong in that it cannot account for the range of aphasic syndromes, (ii) linguistically underspecified to an extent that prohibits contact with the language sciences, and (iii) anatomically underspecified. We briefly summarize some of the central issues that motivate why a new functional anatomy of language is necessary, in the context of introducing a collection of articles that describe systematic new attempts at specifying the new functional anatomy. The major convergent observations are highlighted and the emergent conceptual and empirical trends are identified.
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1. The old functional anatomy of language

Every student of the language sciences has come across the illustration of a left cerebral hemisphere in which there is labeled an inferior frontal area, *Broca's area*, a posterior superior temporal region, *Wernicke's area*, and a connecting fiber tract, the arcuate fasciculus. This anatomic diagram, an image with iconic status in neuroscience, forms the basis of a neurolinguistic model that has informed research for almost 150 years and constitutes the canonical model of brain and language taught across disciplines. The model originated in the 19th century with the influential work of Broca (Broca, 1861, 1865), Wernicke (Wernicke, 1874/1977), and Lichtheim (Lichtheim, 1885). It lost favor, and was, indeed, virtually forgotten over the course of the first half of the 20th century, but was revived and popularized again beginning in the 1960s by Norman Geschwind (e.g. Geschwind, 1965).

The classical conceptualization of the neural basis of language has been immensely useful both as a heuristic model to stimulate research and as a clinical model to guide diagnosis (Damasio, 1992). However, many of the neuropsychological, anatomical, and linguistic assumptions implicit or explicit in the model are known to be problematic, and therefore many researchers have abandoned classical ideas and assumed new theoretical

positions, almost invariably focused on much more circumscribed pieces of the puzzle than was targeted by the classical theorists. This situation has placed us on the verge of throwing out the classical-model baby with the bathwater. The bathwater, of course, is comprised of several details of the model that have failed to stand up empirically (discussed below). The baby is represented by many of the core ideas (again see below), and importantly, the goal of the model, which, to paraphrase Wernicke's (1874/1977) subtitle, is to develop a *psychological model of language on an anatomical basis*. This is a broad goal, and therefore one that is not easily achieved. It is much easier, and arguably more rational, to restrict one's effort to a smaller piece of the problem. But such a strategy carries with it the danger of losing sight of the primary goal, ultimately leading to a fractionated field exhibiting little theoretical convergence. Perhaps we can learn from the classical models that if we must work locally, we should, as the political saying goes, at least think globally. This line of argument applies with equal force to methodological issues. We now have a range of investigative methods at our disposal – hemodynamic imaging, electromagnetic recording, transcranial magnetic stimulation, neuropsychological, and behavioral methods – and it is critical that findings from these various vantage points be integrated.

The goal of this special issue is to aim for theoretical and methodological integration in language-brain research, and hence to refocus some attention on the broader organization. Predictably, the collection of papers falls far short of this goal. However, progress has been made. In the remainder of this paper, we highlight some of this progress and point out some of the shortcomings. We consider the background issues that form the basis for the new and critical work presented in the articles in this volume, starting with a cursory review of the classical brain-language model and some of its implicit assumptions and problems. We end by offering a perspective on what some of the current trends are and where the research program on the neurobiological basis of language might be headed.

2. The classical model

2.1. What's right with the classical Wernicke–Lichtheim–Geschwind model?

The classical model contains many viable and relevant ideas, but the model is often misunderstood by modern researchers (for discussion see de Bleser, Cubelli, & Luzzatti, 1993). We review some remarks by Wernicke (1874/1977) that outline the core components of the model, and highlight the extent to which his theorizing was closely related to many contemporary considerations. These remarks are based on Eggert's 1977 translation of Wernicke's original monograph of 1874 (Wernicke, 1874/1977).

Wernicke, drawing on the work of his mentor Theodore Meynert (Whitaker & Etlinger, 1993), conceived of two language centers, based on the hypothesis that cortex anterior to the Rolandic sulcus served motor functions, whereas cortex posterior to the Rolandic sulcus served sensory functions. According to Wernicke, sensory and motor cortices

served not only in the direct registry of sensory experience or in the direct execution of movement, but also in the memory storage of sensory and motor imagery.

It followed from this general functional-anatomic framework that the anterior motor-speech area identified by Broca a decade earlier was a site for the deposition of motor-images for speech (cf. *Indefrey & Levelt, this volume*), and a posterior area should be the site for the deposition of acoustic images for words (cf. *Boatman, Scott, & Wise, this volume*; *Hickok & Poeppel, this volume*). And, indeed, Wernicke described cases that he argued confirmed the latter site to be the superior temporal gyrus (STG).

Wernicke hypothesized that these two language areas were connected originally as a consequence of a (subcortical) reflex arc active in the process of language acquisition. The child acquiring language, upon hearing a word or syllable, reflexively mimics that word/syllable in speech, which in turn causes the temporally coincident activation of sensory and motor images in the cortex. The temporally coincident activation of cortical sensory and motor memory images of the word, in turn, leads them to become associated directly, via a cortico-cortical pathway that he believed coursed behind the insula.

These acoustic and motor images were distinct from the concepts with which they were associated. According to Wernicke, the acoustic image of a word is a purely auditory entity. The concept, on the other hand, is formed by the sum total of the memory images associated with, say, a particular object. This meant that in order to comprehend the meaning, an association had to be made between the acoustic image and the various sensory memory images representing the concept itself. So not only was there an anatomical connection between the two language centers, but also connections between the conceptual representation systems distributed throughout cortex and the two language centers, both sensory and motor (cf. *Damasio et al., this volume*). The frame of the famous 'house diagram' had been laid out.

Within this model, speech comprehension was seen to involve the activation of an acoustic word image, which in turn activated a distributed set of sensory and motor memory images, which comprised the concept associated with the word. Spontaneous production involved the arousal of a conceptual representation, which in turn activated in parallel both the motor and sensory word image associated with that concept (cf. *Indefrey & Levelt, this volume*). Although Wernicke argued that the conceptual representation made a direct connection with the motor image center and that it was sufficient to activate such an image, he believed that the mapping between concept and motor word image was less precise than that between the concept and the sensory word image (because of its earlier and stronger association laid down in development). Thus, the activation of the sensory word image during production served to facilitate and constrain the selection of the appropriate motor image via the concept-to-sensory-to-motor-word-image pathway (cf. the idea of analysis-by-synthesis, or forward models discussed in much contemporary work). This idea, of course, entails the idea that there is some degree of overlap in systems supporting speech perception and speech production, an idea that has gained recent empirical support (cf. *Hickok & Poeppel, this volume*).

Wernicke could account for the symptom complex of aphasia as it was understood at the time. Damage to the center for motor word images produced a deficit in the production of speech while leaving comprehension intact. Damage to the center for acoustic word images produced a deficit in the comprehension of speech since the acoustic memory

images that linked sounds with their meanings had been lost. Production in such 'sensory' (Wernicke's) aphasics was fluent because the connections between conceptual representations and the motor word center were intact, but speech was disordered because the concept-to-sensory-to-motor-word-image pathway was no longer available to facilitate motor-word-image selection. Wernicke also considered the consequences of disconnection between the two language centers, concluding that it should produce a disorder, which he termed conduction aphasia, similar to that of sensory aphasia except with spared comprehension. That is, production should be disordered because words are selected on the basis of the concept-to-motor-word-image alone, just as in sensory aphasia. But, comprehension is spared because there is no damage to the sensory-word-image-to-concept pathway. Wernicke also presented the first case of conduction aphasia in his 1974 monograph.

Striking about this brief review of Wernicke's work is the extent to which the issues match many modern considerations on cortical mechanisms involved in speech processing. If one considers Wernicke's remarks in the context of the papers in the present volume, one sees foreshadowed many of the leading ideas of contemporary research on the neural basis of speech perception and language comprehension.

2.2. What's wrong with the classical Wernicke–Lichtheim–Geschwind model?

Given that the classical model was so accurate (or prescient) regarding work on speech, where do substantive criticisms of the model arise? There are (at least) three issues. First, the model fails to account for a number of facts regarding the symptom complex of aphasia. Second, the linguistic foundations of the model are impoverished and conceptually underspecified. Third, the anatomical assertions of the model have not held up in light of subsequent observations. We consider each issue briefly.

2.2.1. Symptom complex of aphasia

A number of observations about aphasic symptomatology are not easily accommodated by the model. These include (i) the existence of anomic aphasia, (ii) the fact that Broca's (and conduction) aphasics typically have mild sentence-level comprehension deficits, (iii) that one finds different distributions of paraphasic errors in different aphasic subtypes (for example Wernicke's vs. conduction aphasia), and (iv) the existence of agrammatism in the speech output of some aphasics, to name a few. More generally, the various clinical syndromes were assumed to be homogeneous entities with a largely fixed set of symptoms that could be explained straightforwardly by damage to a single computational/representational system, or the connection between such systems. We now appreciate that clinical aphasic syndromes are comprised of variable clusters of symptoms. The fact that properties characteristic of a given clinical type can dissociate suggests different computational underpinnings, and therefore a much more complex architecture.

2.2.2. Impoverished linguistic model

Some of the shortcomings of the classical model can be traced to its dramatically underspecified model of language. In the oldest conceptions, language was simply fractionated into expression (production) and reception (comprehension), a conceptualization that is obviously too coarse (although it is important to appreciate that the brain systems supporting these functions were not fractionated simplistically into expressive and receptive regions – a common misunderstanding today). Later attempts assumed that 'large scale' linguistic subsystems could be assigned to the relevant areas, such as *syntax* vs. *semantics* vs. *phonology*. What was not seriously considered is that such linguistic domains are themselves not monolithic, but have rich internal structure with numerous subcomponents and computational requirements. Therefore, it is very problematic to assign a label such as *semantics* or *syntax* to a brain area without being explicit that these are subdivided domains with specific computational needs.

2.2.3. Anatomical problems

It has become clear that the classical anatomical assertions are not true. Broca's aphasia is not caused by damage to Broca's area (Mohr et al., 1978). Wernicke's aphasia is not caused by damage to Wernicke's area (defined classically as the posterior third of the left STG) (Bogen & Bogen, 1976; Dronkers, Redfern, & Knight, 2000). Conduction aphasia is not caused by damage to a white matter pathway, arcuate fasciculus or otherwise, and appears not to be a disconnection syndrome at all (Anderson et al., 1999; Damasio & Damasio, 1980; Hickok, 2000; Hickok et al., 2000; Tanabe et al., 1987). Some would argue that aspects of linguistic function, i.e. speech perception, are organized bilaterally rather than unilaterally in the left hemisphere (Hickok & Poeppel, 2000). And there is now good evidence that the classical speech-related regions are not anatomically or functionally homogeneous (Amunts et al., 1999; Galaburda & Sanides, 1980; Wise et al., 2001). Furthermore, modern work has identified areas outside of the classical regions that are implicated in language processing. As is discussed in the contributions in this volume (for example, *Dronkers et al.*; *Ullman, Indefrey, & Levelt*; *Damasio et al.*), there are cortical and subcortical regions that clearly contribute to normal language processing, including the anterior superior temporal lobe, the middle temporal gyrus (MTG), the temporo-parietal junction, the basal ganglia, and many right-hemisphere homologues. Since many areas are relevant in addition to Broca's and Wernicke's areas, it is obvious that the model must be rethought.

In summary, it is now rather uncontroversial that the classical model is (i) empirically wrong in that it cannot reasonably account for the range of aphasic syndromes, (ii) linguistically underspecified to an extent that prohibits contact with theoretical or experimental research on language, and (iii) anatomically underspecified.

3. Sources of progress: linguistics and cognitive neuroscience

Unsurprisingly, progress on brain-language research has been driven by advances in both linguistics and cognitive neuroscience. A major source of conceptual enrichment and

change has been research in theoretical linguistics and psycholinguistics. At least since the 1950s, we assume that there exist many different levels of representation that have independent motivation and their own internal structure. Experimental research in psycholinguistics and neurolinguistics has been (more or less) connected to theoretical progress and has contributed much to our understanding of real-time language processing (Altmann, 2002). Minimally, these lines of work have established that the linguistic computational system – both in terms of its formal organization and real-time processing components – is comprised of many distinct levels that have specialized computational requirements. This imposes serious constraints on the neuroscience of language: it is clear now that coarse categorizations of language functions into phonology, syntax, semantics, or speech perception, lexical processing, speech articulation, syntactic parsing, and so on, are hopelessly underspecified as linguistic concepts to guide brain mapping endeavors. In fact, given our current understanding – where the major debates center on what regions support such putative functions as 'parsing', 'semantics', or the 'perception of intelligible speech' – it is quite clear that we are scarcely more sophisticated linguistically than Wernicke was in the 1870s.

The increasingly articulated linguistic and psycholinguistic models provide one major source (albeit underutilized) for progress in brain-language research. The other major source derives from technical advances. First, the development of structural CT and MRI allowed lesion mapping in living patients, and subsequently PET provided the first glimpses into the normal functioning brain, followed by the development of functional MRI, finally making non-invasive high-resolution brain imaging widely available. Paralleling the development of the hemodynamic imaging techniques was the emergence of multichannel EEG and the advent of MEG, both of which allowed researchers to chart the timecourse of neural events underpinning language processing. The imaging techniques have been used extensively – although we would argue not always effectively (Poeppel, 1996) – and have generated progress in our understanding of the neuroscience of language. The further development of these techniques and the development of new ones (e.g. near infrared spectroscopy, transcranial magnetic stimulation, to name two) will yield further empirical progress.

4. Towards a new functional anatomy of language: the present issue

What sets this group of papers apart and what unifies the selection of articles as a group? What makes the contributions special is that each paper articulates a larger scale model than is typically presented in experimental work. In other words, the authors are putting their cards on the table about their larger perspective – and are therefore, of course, willing to be wrong! But, right or wrong, the broad views developed here at the very least provide hypotheses for future research, and in many cases lay out the agenda for research programs.

Second, the aspect that unifies these papers is that they all build on the rich literature deriving from the neuropsychological deficit-lesion tradition – but extend the empirical base by considering many other sources of data that have not been assessed as deeply

before. In particular, neuroimaging data are evaluated. But beyond neuroimaging, the range of empirical approaches discussed includes clinical approaches such as electrical stimulation mapping and hemispheric anesthetization (*Boatman*), dichotic listening (*Scott & Wise*), and electrophysiological recordings (*Scott & Wise*; *Indefrey & Levelt*; *Hickok & Poeppel*; *Ullman*). In this context one should also consider other recent papers that present large scale integrative models, including papers in the volume edited by Brown and Haagort (1999), and the reviews by Friederici (2002), Kaan and Swaab (2002), and Stowe, Haverkort, and Zwarts (in press). These papers, too, bring an empirically broad perspective to the task of outlining brain-language models that are biologically sensible and theoretically grounded.

The ultimate goal in this program of research is, presumably, to have theoretically precise, computationally explicit, biologically grounded explanatory models of the human brain's ability to comprehend and produce speech and language. Can we succeed with this goal? Certainly not, at least in the near future. The goal here is, as *Scott and Wise (this volume)* state it, "unashamedly phrenological" – which is a necessary step. In some sense, this should be seen as an intermediate problem that forms the basis for subsequent research, in which, once the functional anatomy has been specified, the detailed computational properties of specific brain areas are explored, much as is done in other areas of inquiry, say vision research.

Three of the contributions focus primarily on speech perception, but it is noteworthy that all three also consider the interface of the speech perception system with other aspects of the linguistic computational system and consider the broad implications for the functional anatomy of language. *Scott and Wise's* refreshingly opinionated perspective on speech perception reviews neuroimaging, deficit-lesion, and dichotic listening data to develop a model of speech perception and auditory cognition that is also closely informed by animal data on auditory cortex. They approach the problem from the perspective of the acoustic complexity of speech. Their article plays an important role in that they raise a number of important issues concerning speech theories, the relevance of the concept 'phoneme', the importance of the syllable as a processing unit, and the problems inherent in the deficit-lesion method.

Boatman's article presents a unique approach not otherwise discussed, namely data from electro-cortical stimulation mapping and hemispheric anesthetization (Wada test). Based on patient work, Boatman attempts to functionally fractionate the STG, and the research converges nicely with *Scott and Wise's* approach (although there are disagreements in detail, for example concerning the speech specificity of the left STG and superior temporal sulcus (STS)). Moreover, both papers are careful to connect to the animal literature. Roughly, Boatman argues (i) that left middle and posterior STG are the substrate for acoustic-phonetic processing, (ii) that STG, left inferior frontal gyrus, and inferior parietal cortex support phonological decoding, and (iii) that the interface with lexical semantics is provided by more broadly distributed areas. Her review of hemispheric anesthetization data suggests bilateral involvement for speech, a conclusion that is also supported by *Scott and Wise* as well as *Hickok and Poeppel*.

Hickok and Poeppel further develop a neuroanatomic model first discussed in Hickok and Poeppel (2000) that takes its central idea from the literature on cortical visual pathways. Based on imaging, deficit-lesion, and electrophysiological data they argue that

there are, broadly speaking, two pathways that are relevant to speech perception and language processing more broadly conceived, a ventral and a dorsal pathway dealing with auditory comprehension and auditory–motor interaction, respectively. The framework attempts to bridge gaps between domains of inquiry including speech perception and production, language development, sensory–motor integration, and verbal short-term memory. The proposal is closely related to the conceptualization of pathways presented both by *Scott and Wise* and by *Boatman*. Indeed, there are important convergences and disagreements among these papers. As a collection, these three articles on speech perception proper, together with *Indefrey and Levelt's* article on production, highlight that research on speech is an area of inquiry in which there is striking convergence across recording methods, labs, and experimental approaches. The disagreements (the specificity of left STG and STS; the precise contribution of the right hemisphere areas; the nature of the parallel pathways; the locus of the auditory–motor interface) are of a level of detail and specificity that imply considerable agreement about the fundamentals.

Returning to production, *Indefrey and Levelt* develop a detailed model of the functional anatomy of production based on imaging and electrophysiological data. In an extensive and inclusive meta-analysis of imaging studies they argue for a specific functional anatomy (that converges surprisingly well with the three perception articles) as well as a time-line for speech production. Their review reveals the important role for speech production of the STG, and, crucially, clearly implicates the MTG.

The important role of the MTG identified by *Indefrey and Levelt* is also highlighted in the two deficit-lesion papers by *Dronkers et al.* and *Damasio et al. Dronkers and colleagues* report the results of a deficit-lesion study involving 64 patients with left- and eight with right-hemisphere damage. Their analysis of the neuropsychological data implicates MTG in word-level comprehension, the anterior STG in the construction of basic phrase structures, posterior STG and inferior parietal cortex in auditory short-term memory, and anterior (non-Broca) inferior frontal gyrus (Brodmann's areas 46, 47) in working memory functions. Importantly, based on the test instrument they have used (CYCLE), canonical Broca's area is not implicated. These data, again, converge in important respects with the conclusions drawn by *Indefrey and Levelt* on production data as well as the models articulated by the papers on speech. For example, in addition to the critical role of MTG for word-level processes there is clear involvement of the anterior STG (see, e.g. *Scott & Wise*) as well.

Damasio et al.'s contribution is methodologically closely related to Dronkers et al.'s work. Here, too, a large number of deficit-lesion cases are examined (84 left- and 55 right-hemisphere damage cases are analyzed). Also, both articles are concerned with developing the next generation of lesion reconstruction approaches. In contrast to *Dronkers et al.*, *Damasio et al.* are interested in a particular cognitive operation, recognition and naming of concepts. Therefore, in addition to lesion data, Damasio et al. present imaging data (PET) investigating recognition and naming of categories such as persons, animals, and tools. Their data suggest a segregation of function, primarily in inferior temporal cortex, such that the substrate supporting these conceptual distinctions differs, ranging from anterior temporal lobe (persons) to posterior temporo-occipital cortex (tools).

Interestingly, *Damasio et al.* are also concerned with the important role that experimental tasks play in the generation of neurobiological results. In general,

the nature of tasks and their problematic role, i.e. the role of ecological validity, is a theme that is also discussed by *Scott and Wise* and by *Hickok and Poeppel*, suggesting that it is an issue that worries practitioners with regard to the interpretation of their neurobiological data.

Ullman presents his Declarative-Procedural model, a neurocognitive approach that is designed to make contact between aspects of language and non-linguistic neural functions such as declarative and procedural memory. An extensive review of lesion and imaging data (as well as numerous other sources of data, including data on sex differences as well as normal and pathological language acquisition) suggests that there is a close relationship between the brain systems that drive the different forms of memory and those linguistic computations that have 'declarative' (e.g. retrieval of lexical items) or 'procedural' (e.g. online computation of an inflected form) requirements. *Ullman's* paper makes a notable effort to connect the model to numerous aspects of systems neuroscience.

A brief tour through the major figures of the papers provides a visually striking overview of the research. To obtain a quick and intuitive but very useful impression of the work that is reviewed, summarized, and integrated in the papers in this volume, it is helpful to turn straight to the images. We recommend that the reader study Fig. 1 in *Scott and Wise*, Fig. 4 in *Boatman*, Figs. 1 and 2 in *Hickok and Poeppel*, Figs. 4 and 5 in *Indefrey and Levelt*, and Fig. 9 in *Damasio et al*. Cumulatively, these images summarize an enormous range of data, approaches, and theoretical predilections. Strikingly, the figures, as a collection, illustrate the emergence of consensus.

5. Trends, convergence, and the emergence of a new model

It is impossible – and perhaps even incoherent – to attempt to summarize the set of findings and models discussed in these articles. Nevertheless, there are several convergent observations and hypotheses.

1. Broca's area and Wernicke's area are no longer viewed as monolithic or homogeneous pieces of tissue. Rather, there are attempts to define, subdivide, and functionally interpret both of these cortical regions. It is particularly noteworthy that no paper in the present collection focuses on or attributes any special role to Broca's area or Wernicke's area.
2. The fractionation of STG and its functional role is a very active area of imaging research, with a major proposal being that functionally and anatomically distinct parallel dorsal and ventral pathways originate in the STG.
3. There is a dramatic increase in attention to cortical areas outside the traditional perisylvian language zone. Some of these regions include the middle and interior sectors of the temporal lobe for its role in word-level processes, the anterior STG for its role in the construction of phrases as well as intelligibility, and subcortical structures (basal ganglia, cerebellum) for their role in linguistic computation.
4. There is increasing interest in the relation between perception/comprehension and production and the potential role of posterior temporal and inferior parietal cortex in

the auditory–motor interface. There is a hypothesis that a Sylvian parieto-temporal area (Spt) drives an auditory–motor interface, as well as proposals that areas 7 and 40 perform subroutines of verbal working memory.

5. The right hemisphere, the ugly step-hemisphere in brain-language models, is being rehabilitated. There is broad consensus that, at least in speech perception, the right temporal lobe plays an important role, and, more generally, one of the main consequences of imaging research has been to highlight the extensive activation of the right hemisphere in language tasks. On balance, a modification of the virulent left-hemisphere imperialism characteristic of the field is in order.

6. The future: where have we been and where are we going?

The history of neurolinguistics looks like any other domain of the natural sciences. That is, initially, rather coarse distinctions sufficed to account for the basic phenomena of interest, but as knowledge in the biological and the linguistic domains accumulated, numerous necessary modifications were made as the concepts in both domains became finer-grained. An (admittedly naive) optimistic perspective therefore suggests that all is well and that progress in linguistics and psycholinguistics and parallel progress in neuroscience will continue to lead to periodic improvements and small changes in our models. But will real understanding and explanation emerge? A less charitable view is that the progress of 'normal science' will not suffice and that paradigmatic changes are in the air – or should be. Specifically, the question of 'unification' has been raised (e.g. Chomsky, 2000). Will there be a unified account, motivated by disciplinary and interdisciplinary considerations, which captures both the biological realities and the generalizations accounted for by linguistic research?

A unified account of brain and language is likely to require two things. First, we need linking hypotheses that bridge the conceptual and technical apparatus of linguistics with the machinery of neuroscience, i.e. linking hypotheses that bridge concepts such as 'distinctive feature' or 'phrase' or 'lemma' with the mechanisms of neurobiology (e.g. concepts such as 'receptive field' or 'oscillation'). Second, a deeper requirement, going beyond the postulation of bridging or linking hypotheses, is the possibility of conceptual change in both domains of inquiry. Will linguistics and biology have to modify their conceptual apparatus in order to develop unified explanatory accounts? This is a distinct possibility. Beyond a functional anatomy of language, the modest beginnings of which are sketched out here, we will also require a functional physiology of language, an area that we have not addressed. Future, increasingly unified accounts will present a computationally explicit connection between linguistics, psycholinguistics, and neurobiological mechanisms. The present work simply represents a very first step in that direction by attempting to identify the brain areas that must be included for further investigation.

Acknowledgements

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