Towards a Neurobiology of Language

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The advent and/or improvement of high resolution brain imaging methods over the past two decades – both spatial and temporal – has led to the emergence of an anatomically and physiologically robust human neuroscience. In no area has this been more evident than in the study of human language. A recent congress on the Neurobiology of Language attracted over 500 participants. Many – but not all – researchers in this field take the view that language processing in the brain is implemented by many interacting sensory, motor, and conceptual networks that are not specific to language, but evolved to support many critical features of human cognition, including contextual expectation, statistical inference, sequence processing, error detection and correction, and related computational basics. The neural systems that underlie these computations appear to incorporate a large number of anterior-posterior brain connections along dorsal and ventral "streams". Although these streams each include many individual connections, and contribute to many different functions, some gross functional generalities can be articulated. In this Symposium, we introduce the anatomy of these streams, and then describe several models and/or cognitive functions that support language processing in dorsal and ventral brain networks.

Dorsal and ventral processing streams in the human brain

Ferdinand Binkofski

The distinction between dorsal and ventral processing streams has been elaborated substantially in recent years, spurred by two developments: (1) First is a more detailed description of the multiple neural circuits connecting the frontal, temporal, and parietal cortices; and (2) Second are a number of behavioral observations that the classic "two visual systems" hypothesis needs refinement to accommodate additional assumptions. The notion that there is a single dorsal stream that is specialized for "where" or "how" actions and a single ventral stream for "what" knowledge cannot account for two prominent disorders of action, limb apraxia and optic ataxia, that represent a double dissociation in terms of the types of actions that are preserved and impaired. A growing body of evidence suggests that there are at least two distinct dorsal routes in

the human brain, which we characterize as the "Grasp" and "Use" systems. Both of these may be differentiated from the ventral route in terms of neuroanatomic localization, representational specificity, and time course of information processing. In this talk, we discuss the anatomy and physiology of the dorsal and ventral streams for vision and action, and relate them to the analogous streams for audition, speech, and language.

Neurobiological roots of language in primate audition: Common computational properties

Steven L. Small

Neurobiologically plausible models of human brain function are typically based on detailed animal models. However, while the applicability of this modeling strategy is widely accepted for domains such as vision or audition, its transferability to human language is considerably more controversial. The reason for this perspective – particularly at the level of sentences and above – relates to complex computational properties of human grammars and their purported specificity to our species. It is generally accepted that human speech and language processing is supported by a cortical dorsal-ventral streams architecture that shares many anatomical characteristics with the extended auditory system of nonhuman primates. A postero-dorsal stream connects AC to the posterior and dorsal part of inferior frontal cortex (IFC) (Brodmann area [BA] 44) via posterior superior temporal (pST) cortex, inferior parietal lobule (IPL), and premotor cortex (PMC, whereas an antero-ventral stream traverses anterior superior temporal cortex (aST) to terminate in more anterior and ventral parts of the inferior frontal gyrus (BA 45). Dual–stream models of sentence processing typically assume that the neural circuitry of nonhuman primates is insufficient to support sentence comprehension because of a fundamental difference in its computational architecture that is not simply a matter of degree. They thus posit uniquely human additions to this circuitry in the dorsal stream, which are assumed to have evolved late from a phylogenetic perspective and to mature late from an ontogenetic perspective. In this talk, we suggest that the nonhuman primate dorsal and ventral auditory streams have the necessary mechanistic components to perform sentence and discourse processing, even though the system lacks the necessary quantitative scale to support language.

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Statistical regularities in input: The basis of neural encodings for language

Uri Hasson

The capacity to code for statistical features of language is thought to enable language learning, assist online word segmentation, and form a basis for prediction of subsequent speech input. How does the brain code for the statistical structure of the language stream? I will present recent neuroimaging data addressing this question, and focus on three issues: *a*) Is there a domain general system sensitive to structure in both language-like and non-language like inputs? *b*) Are there separate systems sensitive to different types of statistical information, e.g., marginal frequency vs. transition probability? and *c*) Are different forms of statistical learning engaged depending on whether the language tokens are novel or familiar? The answers to these questions (no, yes, and yes) suggest the existence of distributed, domain-specific systems for encoding statistical structure, with separate brain systems coding for different statistical aspects of the stimulus.

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Context is all: There is no fixed organization of language and the brain

Jeremy Skipper

Is there a ‘center of speech’ in the brain? It is generally (though perhaps implicitly) assumed that there is. In contrast, I argue that there is no core, i.e., fixed region, set of regions, or (dual) "streams" supporting the organization of language and the brain. I suggest that the illusion that there is some core is created by: 1) the wiring of the brain, 2) the methods and statistics used in neuroimaging and 3) the fact that we have not observed the brain during natural language use. Supporting this argument, I show that the same word can have a very different whole brain organization as a function of the type of context that accompanies that word. Context includes both that which is present (e.g., observable speech associated gestures) and that which has been previously experienced (e.g., music, lip movements, and written text repeatedly encountered in the past). I also show that, even in brain regions where activity might be expected to be comparable for a word heard in different contexts, e.g., auditory cortex, it is not. I argue from these results that, rather than being organized around linguistic information *per se*, language and the brain is organized around context. This is because context is necessary for speech perception and language comprehension to occur. Because the context associated with natural language use

is ever changing, so to will the many brain networks that comprise the organization of language and the brain be dynamic.

Context predicts word order processing in Broca's region

Mikkel Wallentin

While famous for its role in language processing, the actual function of the left inferior frontal gyrus (L-IFG) is still highly disputed. In terms of dual stream models, it has recently been argued to be part of the dorsal stream for speech, whereas it has also traditionally been considered as part of the extended ventral visual stream. A number of language processing studies have linked the region to the processing of syntactic structure. Still, there is little agreement when it comes to defining why linguistic structures differ in their effects on the L-IFG. In a number of languages, the processing of object-initial sentences affects the L-IFG more than the processing of subject-initial ones, but frequency and distribution differences may act as confounding variables. Syntactically complex structures (like the object-initial construction in Danish) are often less frequent and only viable in certain contexts. With this confound in mind, the L-IFG activation may be sensitive to other variables than a syntax manipulation on its own. This talk investigates the effect of a pragmatically appropriate context on the processing of subject-initial and object-initial clauses with the IFG. We find that Danish object-initial clauses yield a higher BOLD response in L-IFG, but we also find an interaction between appropriateness of context and word order. Given an appropriate context, the L-IFG activation drops remarkably for object-initial clauses. This interaction overlaps with traditional syntax areas in the IFG. Further, an acceptability study shows that, given appropriate contexts, object-initial clauses are considered more appropriate than subject-initial clauses. The increased L-IFG activation for processing object-initial clauses without a supportive context may be interpreted as reflecting either reinterpretation or the recipients' failure to correctly predict word order from contextual cues. These findings are discussed in relation to the dual stream models.