



Seeking clues in brain development to explain the extraordinary evolution of language in humans



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ABSTRACT

There has undoubtedly been a quantum leap forward in the evolution of cognitive processing in the human brain that has uniquely granted our species the use of syntactically complex language, however, the building blocks are present earlier in evolution suggesting that language may derive from our genes, and thus brains have evolved to embody a knowledge of Universal Grammar. Gene expression changes in development are the most likely to cause such macro-evolutionary alterations in neural circuits, and in this review I explore four areas of development predicted to be of importance. Firstly, there has been an increase in size and gyrification of the cerebral cortex. Secondly, there is increased connectivity between functional areas of the cortex, an expanded role for the subplate in guiding this process, and changes in synapse formation. Thirdly, the role of GABAergic interneurons in modulating functional connectivity has been enhanced and an elaboration in the developmental origins of interneurons may have led to an increased repertoire of functional subtypes. Finally, the development of lateralisation of language function is also briefly considered.

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1. Introduction

1.1. Why look during development?

Whether we take the view that our brains have evolved to embody a knowledge of universal grammar (Chomsky, 2006; Hinzen, 2012) or that language has evolved to fit the functional constraints imposed by the brain (Christiansen and Chater, 2008) or perhaps a bit of both (Pagel and Atkinson, 2008) we can't escape the observation that "human language is spectacularly unique, and spectacularly functional" (Hurford, 2008) giving our species the ability to communicate abstract ideas to each other via an array of sensory modalities (we can listen, read with our eyes or through our finger tips, observe sign language) allowing us to pass on accumulated knowledge. Such adaption has surely required a quantum leap forward in cognitive processing in our species. But where does this quantum leap come from? What, if any, are the fundamental differences in the neural circuitry of the human cerebral cortex and associated structures that make us different from our favourite model organism, the mouse, or even from our primate relatives? Are we merely blessed with a relatively larger cerebral cortex giving us greater processing power, or are there specific enhancements in the way our neural circuits are

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organised that have given us that evolutionary boost? As gene expression changes during development have the greatest capacity to drive macro-evolutionary changes (Carroll, 2008) it is productive to search for specific differences in developmental processes in the human brain, and the cerebral cortex in particular, compared with other species that might give rise to our enhanced cognitive powers (Rakic, 2009). In this article I will briefly explore whether there are any of the building blocks for language circuitry in the non-human brain. Then I will focus on four specific human differences in cerebral cortex development, with reference to their potential influence on language and grammar processing.

1.2. *How brains are organised*

The intuitive viewpoint of most neuroscientists, I would think, is that our brains have evolved a framework to process high level language, rather than our culture having programmed our language capability into our brains as we develop. We know that each individual, except for those suffering a gross environmental or genetic insult, possesses a brain built in development to the same plan. Different functional modules always appear in the same place, connections between areas are universal and the architecture of the brain tissue at the cellular level is the same (Rakic, 2009) although there may be subtle differences in all these parameters that underlie human diversity in intelligence and personality. Furthermore, many similarities with other vertebrate species are readily discernible, including at the level of gene expression (Ip et al., 2010). What is clear is that even the cerebral neocortex, the newest evolutionary addition to our brain and the supposed biological substrate for our cognitive prowess, can be found in rudimentary form in prehistoric reptiles (Northcutt, 1981). It is generally accepted that the layout of the cerebral cortex is determined by the co-ordinated and compartmented expression of genes in time and space at the earliest stages of its development prior to it being connected with by sensory input that could drive its maturation (the protomap hypothesis, Rakic, 1988).

Myriad studies using functional MRI that map brain activity during specific mental tasks to specific cortical areas have demonstrated that there is little variation between individuals in the way the brain is “wired up”. That our brains work in the same way may give rise to the common themes of cultural expression seen in diverse human populations. For instance, geometric patterns that re-appear in many works of art and decoration bear resemblance to the hallucinations generated by altered states induced by migraine or psychedelic drugs (Sacks, 2012). They represent the interpretation by higher cognitive centres of inappropriate activation of assemblies of neurons in primary visual cortex whose normal role is to detect patterns of light and dark present in the visual field. Such neurons are present in other species too. Would they produce the same geometric patterns if they were somehow physically enabled to produce works of art, or do they lack the higher cognitive processing to appreciate these patterns?

In the context of this article, this leads us to the more specific question; does the absence of the ability to produce syntactically structured sequences (whether the sequences are of vocalisations, hand gestures or written symbols) prevent the comprehension as well as the formulation of syntax in non-human species? In humans damage to Broca’s area is classically associated with failure in production by speech of syntactic sentences but also in the comprehension of syntactically complex sentences (Berndt et al., 1997). Broca’s area can loosely be described as being in the motor planning part of the cerebral cortex, spanning premotor cortex and frontal associative cortex (Cepanec and Judas, 2010) which includes mirror neurons which are active both in the enactment and the observation of behaviour (Rizzolatti and Arbib, 1998). Motor planning can be summarised as the organisation of discrete movements into a motor programme such that the movements take place in the right order to produce a purposeful movement. This can be seen as analogous with organising production of words in the right order to produce a syntactical sentence. In both cases, the neural circuits have access to memories of movements or word orders to aid them in assembling the right outputs. Output and recognition of syntax may be inextricably wired into the same circuitry, distributed throughout the left hemisphere but feeding into Broca’s area and nearby structures (Grodzinsky, 2000) and involving mirror neurons (Rizzolatti and Craighero, 2004).

So what are the evolutionary precursors of Broca’s area (associated circuits)? Birds seem to produce syntactically complex learned vocalisations but these transmit only phonological information, recognisable as unique by other birds but without semantic content (Bickerton and Szathmary, 2009). In any case, birds lay a long way from us on the evolutionary tree and any similarities in cognitive processing may be the result of convergent evolution, although it is remarkable that songbirds and humans share certain neural circuitry such as a pallial or cortical – striatal – thalamic loop and direct projections from pallium or cortex to syringeal or laryngeal motoneurons unseen in other birds and primates (Bolhuis et al., 2010; Petkov and Jarvis, 2012) although they may be present to some extent in rodents (Arriaga et al., 2012). This suggests that building blocks for syntactic speech production may have been present early in vertebrate evolution (Fig. 1). Primates certainly produce vocalisations with semantic content, as illustrated by the warning calls of vervet monkeys, for instance, but these have a limited syntactical complexity which is entirely context specific, for instance the nature and location of a predator (Seyfarth et al., 1980). Another consideration is the extent to which different species might be capable of learning complex syntactic sequences even if they cannot produce them.

Baboons trained to learn pair-wise association of symbols presented on a screen will spontaneously select sequences of symbols that possess a recursive, nested structure (Rey et al., 2012). This suggests that baboons can combine complex visual information processing (symbol recognition) with associative working memory (symbol association) to select ‘sentences’ that follow syntactic rules.

Experiments have also been conducted in which sequences of sounds are arranged to conform to the rules of an artificial grammar are presented to primates, followed by sequences that violate these rules. Video recording of head movements, and

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