



What animals can teach us about human language: the phonological continuity hypothesis

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Progress in linking between the disparate levels of cognitive description and neural implementation requires explicit, testable, computationally based hypotheses. One such hypothesis is the **dendrophilia hypothesis, which suggests that human syntactic abilities rely on our supra-regular computational abilities, implemented via an auxiliary memory store (a 'stack') centred on Broca's region via its connections with other cortical areas.** Because linguistic phonology requires less powerful computational abilities than this, at the finite-state level, I suggest that there may be continuity between animal rule learning and human phonology, and that the circuits underlying this provided the precursors of our unusual syntactic abilities.

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'All models are wrong but some are useful'

George Box

Introduction

These are heady times for biologists, with new methods offering unprecedented experimental insight into low-level biological mechanisms. Gene-editing and conditional gene expression allows precise examination of the role of specific genes at particular times and in particular tissues [1]. Optogenetic methods provide exquisite control over the activation or inhibition of selected cells or cell types [2]. **Non-invasive brain imaging allows us to peer into the brains of both humans and non-human animals [3,4,5,6].** Given these massive methodological

advances, it is fair to ask what the payoff has been in our understanding of cognition, particularly complex cognition (e.g., language, tool use or social cognition). The honest answer must be that the payoffs have been modest so far. Even for tiny organisms like the roundworm *Caenorhabditis elegans*, where all 302 neurons are identified and their entire connectome of ~7000 synapses has been known precisely for years [7], neurobiologists are still grappling to understand the computations underlying the worm's 'decision' to move forward or backward [8]. It has even been suggested that this vast factual database has not helped us understand behaviour [9].

When we turn to animal cognition in relation to human language, the situation appears dire indeed. A constant flow of high-profile papers proclaiming animal 'precursors' or abilities 'relevant to' advanced cognition turn out, upon closer inspection, to be either methodologically flawed or of questionable relevance. **This has led some prominent commentators to suggest that this whole line of research may be a dead end, and that studies of animal communication have nearly nothing to teach us about the important aspects of human language [10], or even more critically, that modern neurobiology has no clue about fundamental issues concerning the neurobiological basis of memory [11].**

In this essay **I argue that such pessimism is unwarranted.** Despite the need for more cautious interpretation, studies of animal cognition can play a crucial role in understanding advanced human cognition, and indeed they must play a central role in understanding its neural implementation. **The crucial issue impeding progress at the moment is a dearth of explicit computational models** that are tightly linked to implementational hypotheses via specific algorithmic proposals [12*]. In those few happy areas where such linking hypotheses have been proposed (cf. [Table 1](#) for a sampling), the ultimate payoff has been substantially increased understanding. But without explicit, computational formulations of this sort, interspecies comparisons become subjective, imprecise, and unproductive.

In this paper, I briefly recap a recent hypothesis that specifies in computational and implementational terms the neural basis for phrasal syntax in human language: my 'dendrophilia hypothesis' [17,18*]. This specifies a key difference between humans and other animals, raising the question of how these human-specific dendrophilic (tree-loving) abilities evolved. In particular, what precursor

Table 1

Computational bridging relations: examples of hypotheses that attempt to bridge between cognitive and neural descriptions via explicit computational models.

Task description	Algorithmic level description	Engineering description	Biological implementation
Hebbian learning	Increase connection strength for neurons that fire together	Coincidence detection leads to increased coupling	LTP and NMDA receptors [13]
Binaural sound localization	Compute inter-aural time difference	Delay lines from each ear; coincidence detection	Coincidence cells and delay lines in Nucleus Laminaris [14]
Sound stream segmentation	Multi-scale sampling	Multi-frequency cortical oscillations	Delta, theta and gamma coupling [15,16**]
Hierarchical processing	Context-free grammar	Pushdown automaton (stack)	Broca's area stack for temporal lexicon via arcuate fasciculus [17]

mechanisms were co-opted during human evolution to provide us with these putatively novel capabilities? My answer will be that concatenation and sequencing abilities present in nonhuman animals (sometimes misleadingly termed 'syntax', e.g., 'birdsong syntax') are computationally all that is required for human *phonology* rather than phrasal syntax; and that **human phonology thus relies upon processing mechanisms shared with other species — the 'phonological continuity hypothesis'**. I suggest that these sequential processing abilities were harnessed during human evolution to support *structural* operations over hierarchical structures, becoming essentially 'blind' to sequence ordering, but sensitive to grouping and hierarchical distance. This hypothesis makes multiple testable predictions, and provides a strong computationally and neurally grounded rationale for a research programme that investigates animal phonological abilities (heretofore typically ignored by students of animal cognition [19**,20]).

To forestall misunderstanding, it is important to point out that I am not arguing that a single trait, or neural circuit, is the sole difference granting language to our species. Instead, **I focus here on human syntactic abilities as one important difference between our species and other species that needs to be explained** (cf. [18*,21]). But other differences, for example in the social cognition involved in semantics and pragmatics [22] and vocal learning [23] also needed to evolve after hominins diverged from our last common ancestor with chimpanzees around six million years ago. Syntactic abilities are important, and will be my focus here, but are not the only factor underlying language in our species.

The dendrophilia hypothesis

A core insight of modern linguistics is that hierarchical structure plays a key role in phrasal syntax (i.e., the processes by which words are arranged into higher-order groupings like phrases and sentences, often simply termed 'syntax'). By 'hierarchical structure' I mean any type of nested grouping that can be isomorphically represented by a tree diagram, where a 'tree' is a connected, acyclic graph with a designated root node [17].

Hierarchical structure is powerful because it is flexibly extensible. By generating and combining hierarchical structures, we gain 'infinite use of finite means' [24] in both syntax and semantics: given a finite lexicon, we can build up an unlimited set of hierarchically structured sentences with specific semantic interpretations. **The core linguistic insight [25] is that syntactic rules apply over such hierarchical structures and *not* over sequences of words per se.** Thus, in a sentence like

'Bill, who'd had more than a bit too much to drink with John, kissed the Dean'

'Bill' and 'kissed' can be seen as hierarchically adjacent, despite the many words between them. Because of this, we interpret 'Bill' and not 'John' as doing the kissing, despite the direct sequential adjacency of 'John' and 'kissed'. While modern linguists disagree about many things, there is virtually universal agreement on this point, despite a persistent tendency for those in other fields to conflate syntax with word sequence.

A related formal insight concerns the computational requirements for flexible hierarchical structure processing: a hierarchical system capable of processing arbitrary operations over trees requires computational abilities over and above those characterizing the simplest computational systems, at the 'regular' or 'finite state' level [26,27]. Finite state automata (FSA) can flexibly process sequences, and a single (non-embedded) level of grouping, but cannot deal with more than one level of nesting (and are thus unable to correctly parse the sentence above). **There are multiple well-defined levels of processing above this regular level, including context-free grammars (corresponding to push-down automata) and context-sensitive grammars (linear bounded automata).** I will refer to these as 'supra-regular,' remaining agnostic about precisely where in this framework a particular structure or language lies.

Crucially, all supra-regular computational systems have at their heart a FSA; this finite state machine is then augmented by some additional form of memory, such as a counter, stack, or queue, which enables intermediate

results to be stored indefinitely during ongoing sequential processing. A large formal literature details the computational effects of adding different forms of memory [28,29], but here I will skirt around these issues and simply state that supra-regular processing requires, beyond the core FSA, some additional memory store, such as a stack or equivalent (cf. [17]). This has been common knowledge in computational linguistics for many decades.

A decade or so ago, biologists [5^{••},30–33] began a research programme aiming to augment this formal and linguistic picture by comparing human processing abilities with those of non-human animals ('animals' hereafter). What kinds of computational resources do animals bring to bear when they process sensory patterns? What kinds of generalizations do they make, and what cues are relevant? Results of this research programme have been reviewed in several places [34,35[•],36]. The bottom line is that despite well-attested abilities in multiple animal species on various finite-state grammars, there is no good evidence that any non-human species successfully processes supra-regular grammars. This is true despite some tantalizing initial data on European starlings [31], rendered unconvincing by later analyses and critique [37,38]. So supra-regular processing capabilities appear to represent a clear and well-defined distinction between animals and humans, directly relevant to human language abilities. This is the first, behavioural/computational, component of the *dendrophilia hypothesis*: humans have the ability and proclivity to process input in a hierarchical fashion, requiring supra-regular computational capabilities that are either less developed or entirely absent in other animals.

The next obvious question is 'How are such capabilities implemented in human brains?' Here, decades of work in both aphasia and brain imaging paint a rather clear and consistent picture that Broca's area (i.e., [Brodmann's areas 44 and 45]), via its connections with other brain regions, plays an important role (cf. [39–43]). To give just a few examples, when the size of hierarchical chunks being processed by participants in an fMRI experiment is systematically varied, independent of semantics, increased chunk size leads to a steady increase in the activation of Broca's area [44]. When the syntactic complexity of German sentences is increased by using atypical syntactic framing of the same meaning, Broca's area is preferentially activated for more complex sentences [45]. These examples could be multiplied considerably, and are consistent with the idea that Broca's region plays a central role in processing hierarchical structure during sentence processing in humans.

Furthermore, comparative neurobiological data indicate that Broca's region is one of the most hypertrophied regions in the human brain, both in terms of cortical surface area (nearly 7-fold larger than in the chimpanzee brain [46]) and in terms of its connections to other cortical

regions. Connectivity between frontal and temporal regions in non-human primates is heavily weighted towards a ventral pathway, shared with humans. By contrast, a dorsal pathway linking Broca's region to parietal, occipital, and temporal regions, the 'arcuate fasciculus', is uniquely strongly developed in humans [47]. Experiments contrasting simple sequence processing with hierarchical processing show a specific reliance of the latter on this novel dorsal pathway [48]. Direct comparisons of monkeys and humans processing auditory sequences found Broca's activation, in humans only, for sequences demanding simultaneous attention to pattern and number [5^{••}]. Thus Broca's area both plays a critical role in hierarchical processing and is uniquely well developed in our own species relative to chimpanzees and other primates.

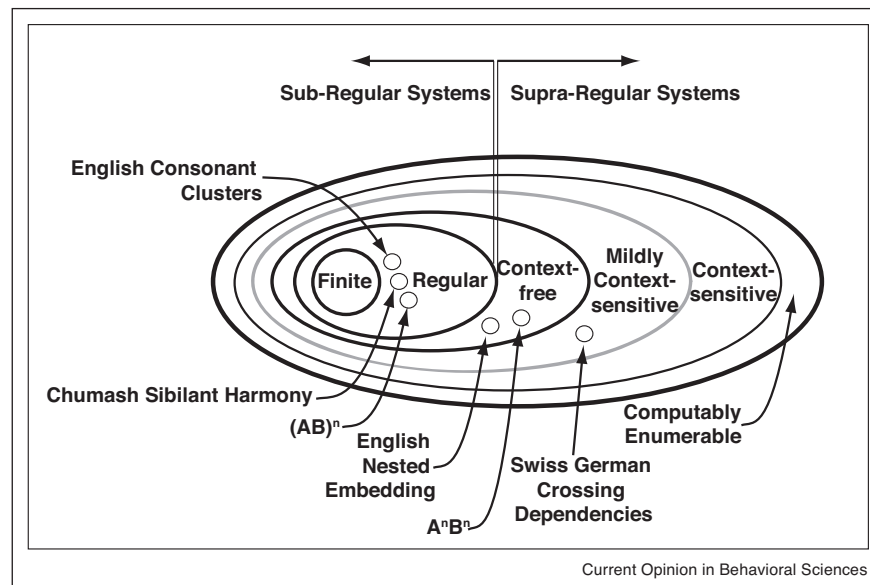
This led me to propose the second, implementational, component of the dendrophilia hypothesis: that the accessory memory (stack or equivalent) required for supra-regular processing of hierarchical structure is implemented in the neural circuit centred on Broca's region [17]. This provides a link between what Embick & Poeppel call the computational/representational level and neurobiology [12[•]]. This Broca's/stack hypothesis leaves open two more specific possibilities. Either Broca's represents a single general-purpose stack, able to store intermediate results for any hierarchical computation, or it incorporates multiple specialized stacks holding different types of material, such as syllables (for phonological grouping), words and phrases (for syntactic structure) and semantic constituents (for semantic interpretation). The second hypothesis, at present, seems more likely to me and is consistent with the suggestion that Broca's region represents a general 'unification space' with sub-regions specialized for particular linguistic processing substrates [49]. Also consistent with this hypothesis is the finding that only sub-parts of Broca's region are activated in specific linguistic tasks [45] and that this region is distinctly parcellated, based on receptor-based mapping [50,51]. More research is required to resolve this open issue about the number and nature of stacks in Broca's region.

In summary, the dendrophilia hypothesis provides both an explicit computational characterization of how the abilities underlying human phrasal syntax differ from animal sequence-processing abilities and a specific implementational model of how this difference is implemented in the human brain. However, as it stands, the dendrophilia hypothesis leaves open the question of precursors, that is, from what pre-existing neural and behavioural basis were these putatively species-specific capabilities derived? I will now address this question.

Phonology versus syntax: concatenation versus embedding

Although any rule-governed activity can be captured by some grammar, it has been convincingly argued that all

Figure 1



The extended formal language hierarchy. A visual representation of some key components of the formal language hierarchy (aka 'Extended Chomsky Hierarchy'), showing where different exemplary linguistic phenomena lie in terms of computational complexity. Crucially, phonological phenomena all lie somewhere in the sub-regular region (meaning they can be computed by some finite state automaton) while many syntactic phenomena require a more powerful system (a pushdown automaton or better). Modified from Ref. [53].

phonological phenomena in human natural language can be processed at the regular level [52,53], while supra-regular grammars are needed to deal with phrasal syntax. This key distinction is illustrated, mapped on to the formal language hierarchy, in Figure 1. But how are these abstract computational differences implemented neurally?

It has been suggested on formal grounds that the computational difference between phonology and syntax could boil down to a difference in the combinatoric operation required, changing the type of structures operated upon [54]. In phonology, the fundamental operation is concatenation over strings, defined as serial sequences of items. In syntax, the fundamental combinatoric operation is *hierarchical embedding of nodes in a tree structure*. The key syntactic dimension is thus the vertical parent-child relation (aka the dominance/subordination dimension), rather than the 'sister' relations between adjacent terminal nodes representing words or morphemes. Discussions of the 'chain of command' ('Susan oversees Sam oversees Sally') or ancestry ('Adam begat Seth, and Seth begat Enos . . .') imply such a vertical readout of a hierarchical combination of elements.

Extending this idea in a neural direction, I suggest that our ability to process hierarchical structure required the conversion of computational circuitry competent at sequential processing into a circuit specialized for

hierarchical processing in this vertical dimension (for potential sequential precursors see [5^{••},6[•],16^{••},42]). By this hypothesis, our massively expanded Broca's area allows us to implement supra-regular processing via its robust dorsal connections to parietal and temporal cortex (cf. [55]). That is, human brain evolution 'hijacked' pre-existing primate sequencing capabilities and simple sequential grouping capabilities already present in our common ancestor with chimpanzees, and modified them to implement hierarchical multi-level grouping. Specifically, I suggest that the syntax/phonology distinction arose via a duplication of regular-level sequential circuitry, followed by a differentiation of these circuits to focus on hierarchical structure (and to be relatively 'blind' to sequence). However, the circuitry necessary to recognize items and process sequences, requiring only finite-state resources, and implemented mainly via ventral pathways [39], stayed essentially the same. Thus I hypothesize that the finite-state machinery at the heart of any computing system changed very little ('phonological continuity') while the novel 'stack' component needed for dendrophilia, instantiated in Broca's area via its dorsal connections to the parietal and temporal cortices, arose via neural circuit duplication and divergence.

Such *duplication-with-differentiation* events are known to play an important role in molecular evolution [56,57], and have been suggested to play an evolutionary role in

neural diversification as well. For example, trichromatic vision in many primates may result from a gene duplication of a photoreceptor pigment gene and subsequent differentiation into long-wavelength and middle-wavelength variants [58,59]. Neurally, Jarvis and colleagues have suggested that the song system in vocal learning birds results from duplication and differentiation of general motor system circuitry [60,61]. Friederici and colleagues suggest that, in addition to the ventral pathway required for sequential processing, there are in fact *two* dorsal pathways: one present at birth and required for vocal learning, and a later-maturing second pathway specifically involved in supra-regular syntax [55,62,63]. Finally, it has recently been proposed that the novel dorsal human laryngeal motor cortex results from a duplication and differentiation of the ventral laryngeal cortex shared with other primates [64^{*}]. Thus, numerous hypotheses have the common theme of duplication of either genes or neural circuits (perhaps both), with subsequent differentiation.

The phonological continuity hypothesis

The evolutionary scenario above suggests that human and animal capabilities in the sequencing and simple grouping domain are closely related, and rely on homologous neural circuitry (cf. [65]). This is consistent with well-documented behavioural facts: animals are able to process sequences, understand serial concatenation and master various regular-level grammars [35^{*}]. I thus propose the *phonological continuity hypothesis* (PCH): ‘humans share the processing capabilities required to deal with regular-level sequential processing, and thus phonology, with other animals, and these shared capabilities are implemented in homologous neural processing algorithms and circuitry’. This strong phrasing implies that some nonhuman animals should possess the processing capabilities underlying any known phonological phenomenon (say, Chumash sibilant harmony, or stress phenomena in metrical phonology), and that these are implemented using homologous neural mechanisms. The argument that our ‘sequential brain’ is shared with other species is of course a strong claim: its purpose is to focus the attention of phonologists and animal-cognition researchers on this important but almost completely neglected research topic.

Two immediate potential objections to this strong wording concern absence of evidence and defining homology. It is of course a challenge to demonstrate the absence of any ability — the fact that some individuals fail to learn something in some experimental context is a null result that could stem from experimenters’ ineptitude at designing the experiment and/or participants’ lack of motivation, rather than true inability. Thus, a convincing demonstration of inability should involve paired tasks that differ in only one key respect, where subjects succeed on the control task and fail on the focal task (e.g., [30]) — only then can we conclude that experimental conditions were

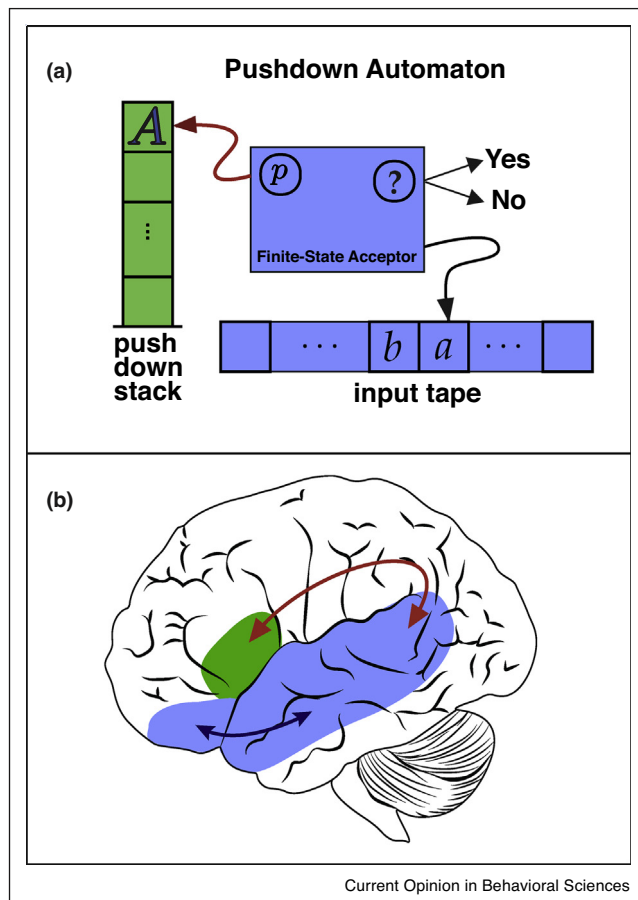
adequate for learning and generalization by members of this species, using this category of sounds and experimental paradigm. The more closely the two tasks are matched, the more convincing is the argument that failure on the focal task indicates inability, particularly if this failure continues even with training or extra data presentation.

Regarding homology, it is always possible that two species accomplish the same task using drastically different algorithms or neural mechanisms, so behavioural success would be only one criterion for defining ‘continuity’ by the PCH; homology is another key requirement. While this might seem to require an exclusive focus on nonhuman primates or mammals, I think such a focus would be premature: birds are often more tractable study organisms for auditory tasks, and many aspects of the avian brain are indeed homologous to those of mammals despite superficial differences [66–68]. There are few grounds at present for believing that the ‘sequential brain’ underlying finite-state processing is limited to primates or mammals (cf. [36,69,70]), and arguments for convergent evolution in birds and mammals are premature without a better understanding of such processing in more basal vertebrates (e.g., non-avian reptiles like crocodilians).

It is worth emphasizing that the PCH adopts a quite literal viewpoint concerning formal language theory, and this is at variance with some traditional (and perhaps more intuitive) notions about the phonology/syntax distinction. Traditionally, linguistic sub-disciplines like phonology, syntax and semantics are defined based on the *atoms* of computation (the ‘alphabet’ or ‘lexicon’ over which operations occur): phonology over features and syllables, syntax over morphemes and phrases, and semantics over meanings and entailments. But formally, ‘grammars’ (systems of rules) are required at each of these levels of linguistic structure. The key processing distinction between phonology and syntax concerns regular versus supra-regular computations, rather than the atoms that are combined by these operations. Because every supra-regular pushdown automaton has, at its heart, a regular finite-state automaton, syntactic processing involves sequencing plus additional storage (the stack or queue component of supra-regular automata). Thus, the PCH specifically suggests that both phonological processing *and* the regular aspects of syntactic processing should be shared with other species, and remains agnostic about whether the items being combined are syllables or morphemes or indeed musical notes or visual icons. This proposed mapping of the formal automaton onto proposed neural circuitry is illustrated in Figure 2.

My fundamental goal in proposing the PCH is to help isolate explicitly defined and experimentally tractable phonological phenomena that animals *can* master, and to determine the underlying computations, in direct comparison with humans (cf. [6^{*}]). This would enable

Figure 2



Mapping regular and supra-regular processing components onto the brain. Panel (a) shows the components of a pushdown automaton, the simplest supra-regular computational model; (b) shows a human brain with postulated color-coded equivalences. The phonological continuity hypothesis suggests that sequential processing at the finite-state (sub-regular) computational level is accomplished via a fronto-temporal circuit connected via the ventral pathway shared with other primates (b, blue), while the auxiliary memory (pushdown stack) required for supra-regular processing is implemented in Broca's region of the inferior frontal cortex (b, green), via dorsal connections strongly developed only in humans (red arrows).

neural investigations of the underlying mechanisms, providing a firmer basis to specify what, precisely, needed to change during human evolution. Far too little is known, at present, about animal phonological processing abilities to make any pronouncements at present, but to the extent that the PCH is correct, everything we learn about animal phonology and its neural implementation would have direct payoffs in our understanding of human syntactic processing.

Conclusion

These are exciting times in neurobiology, given the astounding power of modern methods to fuel increased

understanding of low-level neural implementation. But applying these tools to topics relevant to the biology and evolution of language remains an important challenge. If, as many researchers have suggested, human syntactic capabilities really are unique, it may appear to doom all studies of 'animal syntax' to irrelevance. I have argued above against this pessimistic view, and outlined a productive middle road for future research, which is based on explicit computational considerations and is consistent with data from linguistics, animal cognition, and neuroscience. The PCH lays out a panoply of clear testable predictions and provides the starting point for a research programme that offers a way out of this apparent impasse. Even if, as I suspect, some details of this model turn out to be wrong, I predict that the model will at least be useful.

Conflict of interest statement

Nothing declared.

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