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Combinatorial capacities in primates

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Do primates have syntax-like abilities? One line of enquiry is to test how subjects respond to different types of artificial grammars. Results have revealed neural structures responsible for processing combinatorial content, shared between non-human primates and humans. Another approach has been to study natural communication, which has revealed a wealth of organisational principles, including merged compounds and sequences with stochastic, permutated, hierarchical and cross-modal combinatorial structure. There is solid experimental evidence that recipients can attend to such combinatorial features to extract meaning. The current debate is whether animal communication can also be compositional, that is, whether signallers assemble meaningful units to create utterances with novel meanings.

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Introduction

Syntax is one defining feature of human language and part of our uniqueness, which raises questions about its nature and evolution [1,2]. In one view, syntax refers to the ability ' . . . to make infinite use of finite means' [3], a pragmatic approach by which linguistic conventions function to achieve social goals [4]. In another view, syntax is the ability to organise and represent mental content in a hierarchical, recursive way, a computational system that generates internal representations [5]. Syntax is also about recognition, which enables humans to discriminate legal from ill-formed sentences not conforming to linguistic conventions and to apply them to form novel, legal utterances [6].

The ontogeny of syntactic skills in humans is still debated, in part because it is difficult to understand the underlying cognitive operations and to determine whether they are language-specific or domain-general (see Mueller *et al.*; Gervain, this volume). An early view has been that human infants possess an innate, universal grammar module that drives language acquisition [7]. A recent embodiment of this hypothesis is that this module is a single powerful operation, 'merge', which combines lexical/conceptual objects into sets [8]. When infants acquire language they use this innate operation, merely adjusting the parameters to their respective language based on the input they receive. Alternative models propose that grammatical competence cannot be reduced to one core operation, but is acquired gradually, in conjunction with an asymptotically growing reference library of speech utterances, accessed by both general-purpose and language-specific rule-based systems that recognise legal combinatorial structures [9•,10]. With this, language learners can go beyond the utterances they have heard and create unbounded linguistic schemas [6, p. 70]. The debate thus amounts to whether syntactic competence is acquired by manipulations of symbols or by general purpose, including statistical learning not specific to language, but closely dependent on cognition and memory for acoustic or other forms of input.

The purpose of this position piece is to provide an update on the combinatorial competence of non-human primates. How extensive are combinatorial and compositional phenomena in non-human primate communication and what is their importance for understanding the evolution of syntax, a core intellectual capacity of humans?

Recently, there has been resurgence of scepticism about the relevance of animal communication studies for understanding language evolution, and especially syntax [11], but this is mainly based on the controversial assumption that the only relevant feature of syntax is generativity. An alternative hypothesis suggests that everyday language use is not very generative at all, but based on accessing prefabricated phrases from a vast stock. Although such utterances may be described in terms of their syntactic structure, language users do not normally generate any of them, but deploy them 'wholesale' in adequate situations. If this view is correct, then evolutionary investigations of syntax should primarily focus on non-generative, combinatorial systems, as frequently seen in animal communication.

Artificial grammars

One way to study the nature and evolution of syntax is to investigate how subjects learn and interact with artificial grammars [12]. The basic idea is to expose subjects to a training phase during which stimulus sequences are presented, but without explicitly highlighting the underlying organisational structure. Subjects are then exposed to a test phase, during which they can apply any acquired 'rule-based knowledge' of the structure to unfamiliar sequences. The technique has been used to investigate cognitive capacities within and across species, and in humans it can be used to understand what parts of the brain circuitry are involved in (artificial) grammar processing [13]. For instance, rats that have learned simple order rules, such as XYX, XXY, or YXX, can determine whether or not novel stimulus sequences comply to these patterns [14]. Various primate studies have used other paradigms, showing, for example, that monkeys can learn to use patterns akin to morphological markers (e.g. English past tense), indicating that the required perceptual and memory capacities have evolved before language [15].

One particularly influential line of research has been to devise artificial grammars along the 'Chomsky hierarchy' with increasing grammatical complexity [16]. Here, monkeys have managed to learn regularities across adjacent and non-adjacent units from finite-state grammars but failed to extract patterns at higher 'phrase structure' or 'context-free' grammars [17•,18]. However, an exclusive focus on primates for evolutionary arguments can be dangerous, as demonstrated by a study with European starlings that recognise patterns more complex than the ones with only adjacent relationships (which tamarin monkeys can learn [19,20]). Also, research with mixed complexity artificial grammars has compared humans and monkeys to find that many humans also struggle with non-adjacent relationships when adjacent relationships are more salient [21].

Artificial grammar paradigms have been very effective in highlighting the brain circuitry involved in processing sequences with different forms of dependencies. For instance, EEG event-related potentials have been compared between macaques and human infants and adults when responding to violations in artificial grammar sequences [22,23]. Furthermore, functional imaging has identified counterparts in human and macaque brains for processing adjacent sequencing dependencies [24•], an initial stage of syntactic processing in some neurobiological models of language [25,26]. These studies have generally supported the notion of evolutionary continuity at certain levels in combinatorial capabilities and of brain structures that support cognitive domain-general processes not specific for language [27].

The weakness of artificial grammar studies is that they are typically based on stimuli with no ecological or social relevance. Subjects are tested with simple sound sequences, which require auditory pattern recognition but are devoid of meaning. Although some linguistic theories stress that syntax should be investigated as divorced from semantics [5], this is unlikely the case during natural acts of communication [28]. For evolutionary considerations, it is equally important to understand signal combinations and compositions during natural social interactions.

Natural grammars

Duality of patterning

In human language, generativity is often highlighted as the pivotal feature, which is visible at two different levels. First, all languages build on repertoires of (meaningless) phonemes (expressed to different degrees across languages) by which meaningful *combinations*, that is, morphemes or words, are generated in compliance with language-specific combinatorial rules. Second, these phoneme combinations are then further assembled into higher-order *compositions*, that is, phrases or sentences. For compositionality, a key point is that the meaning of a composition can be systematically derived from its parts *and* the rules that combine them [29] (see Fitch, this volume). Although the 'duality of patterning' (or 'double articulation') interpretation of language has been a very useful heuristic, it is also a gross simplification of reality because of the deep, hierarchically layered relationships in sentences [30,7] and, crucially, of questionable use for evolutionary studies of animal signals. For example, linguists have long realised that phonemes are abstract constructs that are difficult to ground in the acoustic reality of speech, and that they sometimes carry natural meaning by being linked to mental concepts [31]. Moreover, there are countless examples of linguistic structures at intermediate stages [32], such as patterns in emerging sign languages, idioms, some affixes, which further undermines the notion of duality.

Combinatoriality

Merged compounds

One of the first systematic studies on primate 'syntax' was on wedge-capped capuchins, reported to merge four different call types into larger compounds [33]. No systematic analysis of function has been made so the current interpretation is that compounds are 'online' readouts of conflicting motivations. Similar reports exist on gorilla close calls, which can be given singly or as non-random compounds [34,35].

Chimpanzees pant hoot calls may also qualify as compound calls, consisting of four units; introduction, build-up, climax and let-down, always produced in this order (Figure 1). Although not yet studied systematically, the four units almost certainly contribute to other constructions in chimpanzee vocal behaviour and can be produced as standalone signals (P Fedurek, personal communication). In a study using machine learning, it was demonstrated that the four units convey information on caller identity, rank and age, and on the external event [36].

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