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What birds have to say about language

Tiffany C Bloomfield, Timothy Q Gentner & Daniel Margoliash

Controversy surrounds the suggestion that recursion is a uniquely human computational ability that enables language. A study now finds this ability in a songbird and takes steps toward a model system for syntactic competence.

Human language is an extreme specialization, and its evolutionary history remains shrouded in mystery. The animal kingdom is replete with specializations, and these are appropriately studied from an evolutionary and comparative perspective. This core principle of biological investigation has been more controversial, however, when considering that most human of abilities, language. Nevertheless, language requires competence in several domains, and animals may have more competence in some of these than has previously been appreciated[1]. A study by Abe and Watanabe[2] investigates an important aspect of our language ability, syntax, including the putative 'uniquely human' ability of recursion. Their results demonstrate a broad syntactic competence in a songbird species, as well as the suitability of their approach to understanding complex behavior and its development. They also identify an important brain pathway underlying this syntactic competence, establishing a major new line of inquiry in the fledgling field of biolinguistics.

Many theories focus on syntax as the core driver of language productivity, the ability to produce a vast set of utterances using a limited number of words. Hauser, Chomsky and Fitch[3] reviewed a substantial body of evidence that animals share many cognitive capabilities relevant to the study of language, concluding with the proposal that syntax is special. Specifically, these authors argued that humans uniquely apply the computational capacity for recursion to vocal behavior. This hypothesis, if true, would diminish the value of animal models in the study of language and would confirm a central tenant of Chomsky's tenaciously held view setting human language fundamentally apart from all other animal behavior.

One approach to this problem has been largely descriptive and analytical. Language is hierarchical, allowing a linguistic phrase to itself contain a phrase of the same type. A recursive process—one that invokes itself, repeatedly operating on its own output as input—would be a particularly compact computational approach to creating such structure. Such solutions are attractive in certain classes of computational problems for which the nesting is deep. The archetypal supporting case is when the recursive structures are 'center-embedded'. But in human languages, center-embedding, which for example occurs when clauses, such as the one, which is difficult to understand, that you are reading, are nested in a sentence, is rarely seen beyond a depth of three[4] (**Fig. 1**). Nevertheless, a theoretical argument about the extensibility of sentences has motivated Chomskyan linguists to conceive of a sort of Platonic human recursion machinery, capable of infinite depth of nesting ("competence"), but constrained by human output capacity ("performance")[5]. The conjunction of these two hypotheses (infinite recursion and the distinction between competence and performance), both necessary to explain the observed human behavior, is awkward.

An alternative approach is empirical: to investigate other species' abilities to learn recursively embedded structures to a level similar to humans'. To do this, Abe and Watanabe[2] used a habituation procedure with Bengalese finches (*Lonchura striata* var. *domestica*), a songbird that sings syntactically varied songs consisting of stereotyped 'syllables'. In one set of experiments, Abe and Watanabe[2] exposed the finches to an artificial grammar containing center-embedded structures. To create this grammar, Abe and Watanabe[2] defined three classes, A, C and F, consisting of four birdsong syllables each. The four A syllables were each matched with a particular F syllable. Interposed between them was a 'C phrase', which was either any single C syllable or another matched A-F pair. During exposure, the finches heard every possible grammatical string consisting of ACF, and about half of the possible A A′ C F′ F stimuli. During testing, the finches heard novel grammatical A A′ C F′ F strings, as well as sequences that were ungrammatical. By counting shifts

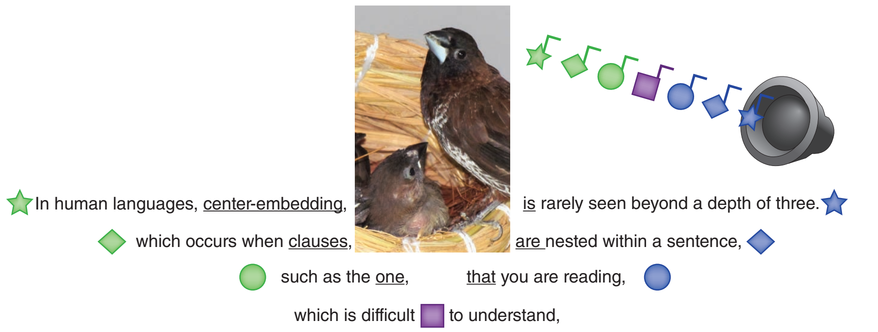

Figure 1 A new form of nesting behavior in birds. This example English sentence from the main text contains deep center-embedding. Each level forms a complete phrase or sentence, which is modified by the embedded phrase on the line below it. A word (underlined) on the right half may correspond to a word on the left half, an example of a long-distance dependency. The colored symbols (after ref. 2) indicate the analogous dependencies in the artificial language tested with the Bengalese finches, although in that case they represent not English phrases but Bengalese finch 'syllables'. Matched shapes indicate the dependencies; matched colors indicated the same phrase type (an A, C or F phrase; see text), a feature not captured in the example sentence. Photo courtesy of Kentaro Abe.

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in their call rates to the test strings, Abe and Watanabe[2] could tell whether the finches detected a difference between the test stimuli and their habituated grammatical stimuli.

The results revealed a striking sensitivity to the recursive structure of the grammatical strings that the finches were exposed to. The finches showed no change in calling in response to familiar strings or novel grammatical strings. However, they decreased their calling when they heard ungrammatical sequences, including sequences whose only violation was an incorrectly matched A-F pair. Even more notable, when Abe and Watanabe[2] embedded an extra C phrase, resulting in A A′ A′′ C F′′ F′ F sequences, the birds again reacted to only those sequences with grammatical violations, not to the longer grammatical sequences, even though there are many ways in which these sequences differed from the habituation set. Accounting for correct generalization in the face of many possibilities, sometimes known as the 'poverty of the stimulus' problem, has been an important motivator for the idea that humans have innate language-specific expectations[6]. Finches have no such expectations, and some aspects of their general syntactic ability seem to require experience (see below). Nevertheless, the finches make the correct syntactic generalizations from a seemingly impoverished input, without access to a special human innate endowment.

In all, this experiment substantially challenges the human uniqueness of the ability to represent recursive structure[3]. Although a previous study[1] also found sophisticated pattern-processing abilities in a songbird, consistent with a recursive structure and comparable to known abilities of humans on an identically structured artificial grammar task[7], Abe and Watanabe's results[2] are the first demonstration that this ability extends to structures requiring long-distance matching of syllables.

Two more experiments investigated other aspects of syntactic complexity. In one, Abe and Watanabe[2] investigated the ability of finches to detect (artificially created) sequence modifications to natural conspecific song. By comparing many different modifications, they found that the finches' responses were not explained by any one local sequence change, suggesting interesting complexity in their natural song representation. In the other experiment, Abe and Watanabe[2] adapted an earlier procedure[8] that compared learning of phrase structure grammar in two conditions, when the phrases did or did not contain strong predictive dependencies. The Bengalese finches learned only in the former case. The previous study[8] examined both human infants and cotton-top tamarin monkeys; it is intriguing that the finches' performance was more similar to that of human infants than that of the tamarins. However, perhaps the main conclusion to draw from the shared difficulty with nonpredictive phrase structures is that some constraints, as well as abilities, might be shared. Languages might be built to take advantage of domain-general, presumably prelinguistic, sequence-learning abilities[9]. The cross-species results lend credence to this and further emphasize the value of a biolinguistic comparative approach to language.

Having established sensitivity to syntactic complexity, Abe and Watanabe[2] exploited their animal model to investigate the underlying developmental, social and neural contributions. Notably, they found that the finches' sensitivity to the experimenter's subtle perturbations of a conspecific's song sequence requires social exposure to normal song, whereas rapid learning of the predictive phrase structure dependencies in the artificial grammars follows an invariant developmental time course. These results suggest that finches make use of statistical information in their environment to distinguish among different patterns of sounds, including conspecific songs. For these behaviors, the questions of which features are innate and how social interactions influence development are now open to experimental verification.

Abe and Watanabe[2] gained additional insight using a lesion approach. Lesions that included the lateral magnocellular nucleus of anterior nidopallium (LMAN), the output nucleus of the songbird's basal ganglia, disrupted both the predictive phrase structure and the sequencing of conspecific song demonstrated in the behavioral experiments. We do not yet know what specific pathway is involved, as the lesions may have involved more than just LMAN. And we do not know whether this part of the brain is necessary for learning center-embedded grammars, as those behavioral tests were not attempted in the lesioned birds. But given LMAN's apparent involvement in general syntactic processing, it is a strong candidate. In humans and other animals, basal ganglia pathways are involved in the sequencing of behavior. The basal ganglia have been suggested as a site of syntactic processing in humans[10]. The finch lesion results help to further focus attention on such propositions.

Abe and Watanabe[2] make an important contribution to the ongoing debate about human language uniqueness. But their results go further, examining syntactic complexity at several levels. Thus, beyond consideration of the theoretical framework arising from the Chomskyan view of recursion, the real power of this and other studies of comparative language mechanisms lies in identifying not what is unique but what is shared. Abe and Watanabe[2] have established syntactic complexity in a way that profitably relates to a variety of empirical results in humans. Elucidation of the neural mechanisms of syntactic complexity, wherever the exact limits of those abilities may lie, is now within reach. Indeed, any such limits may also be relevant to human learning, as humans do not automatically discover recursive structure[11,12] and in fact have only succeeded on matched recursion at the level of complexity shown by the finches with additional learning cues[13,14]. One possibility is that syntax and semantics are linked in humans, so humans are not practiced at noting long-distance correlations in the absence of semantics. Semantics may not exist at all for the finches, which could free the birds to be better syntactic processing machines. Perhaps songbirds are closer to the Chomskyan ideal of possessing an independent syntactic processor than are humans.

Whether or not one considers the hypothesis about the unique place of recursion to be substantively eroded by this demonstration, the contributions of the current study[2] toward a science of biolinguistics should be welcomed by all, forging a new connection between even the most complex human behaviors and organismal and evolutionary biology. From the biological perspective, hypotheses distinguishing human behaviors from those of other animals should account for the massive capacity of human brains. Undoubtedly, some will point to yet another untested capacity as 'the' crucial component of language. But perhaps this is a good time to reconsider whether attempting to distinguish between qualitative and quantitative differences is helpful if the quantitative advantage is vast[15].

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

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