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From bird calls to human language: exploring the evolutionary drivers of compositional syntax

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Compositional syntax, where lexical items are combined into larger units, has been assumed to be unique to human language. Recent experiments, however, showed that Japanese tits combine alert and recruitment calls into alert-recruitment sequences when attracting conspecifics to join in mobbing a predator. We speculate that such call combinations are favoured when: Firstly, callers and receivers have shared interests in exchanging information; secondly, species produce different types of calls in different situations, leading to distinct behavioural responses in receivers; and finally, complex situations exist in which receivers benefit by combining two or more behaviours. These preconditions were also present in human ancestors. Thus, future work on bird calls may provide insights into the evolution of compositional syntax in human language.

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Introduction

Language is a central and defining human feature [1•]. Its expressive power arises from combinatorial abilities, allowing us to produce meaningful words and sentences from a limited set of meaningless elements (phonemes) and meaningful units (words) [2,3]. In addition, grammatical rules, such as word ordering rules, allow us to distinguish between alternative meanings, such as in the famous example 'man bites dog' versus 'dog bites man'. Thus, grammatical rules efficiently expand the number of possible meaningful phrases from a limited set of units. The evolution of such rules should be promoted when a large number of messages are required and there are production and/or cognitive constraints on the number of meaningful units [3]. However, the uniqueness of human language makes it difficult to understand the evolutionary drivers that lead to essential features of language, such as syntax and compositionality (see Table 1 for definitions), particularly if these features indeed evolved uniquely in the hominid lineage, as suggested previously [4]. Recent studies in birds and primates (see Zuberbühler, this issue) have challenged this assumption. Experimental and observational studies in birds revealed that they can combine phonemes into meaningful calls [5–7], and that different meaningful calls can be combined into phrases where the meaning is a reflection of the parts and the order in which they are combined (corresponding to compositional syntax in language [8••], Table 1). Here we review the current knowledge about this feature in birds, and speculate which factors may have driven the evolution of this feature, and thus, may contribute to understand language evolution.

Bird vocalisations: more than just singing and twittering

Researchers interested in language evolution have largely focussed on bird song. Like human language, song is at least partially learned (i.e. song templates are modified based on input from a tutor), and some species have songs that are hierarchically organized and combine a high number of different elements [9]. Moreover, a parallel set of neurological modules and processes are involved in learning and production of language and song [10,11]. Despite these similarities to language, songs are assumed to convey a limited number of messages to receivers (mating status, individual quality, population or group membership [9]). Although some song elements may communicate distinct messages addressing different receivers (mating partners, competitors, see [12]), most individual elements of a song are thought to be meaningless on their own. Also, the order of the individual song elements is not thought to convey information *per se*, but may reflect local traditions or is a means to match the structure of the song of a neighbour [13]. While most songbirds sing [9], almost all bird species give calls. Like songs, calls can be combined into structured units, but

Table 1

Terminology and definitions used in the paper.

What	Definition	Language example	Animal example
(a) Basic linguistic concepts			
Phonology	Meaningless elements are combined into meaningful elements (calls, words)	c+o+m+e = 'come'	Bird song elements [49], AB (flight call), ABA (prompt call) calls of chestnut crowned babblers [5]
Syntax	Meaningful elements are combined into meaningful phrases, according to grammatical and pragmatic rules	come + here = 'come here'	ABC–D calls of Japanese tits [20••]: alert + approach = approach while scanning to mob a predator
(b) Combinations of at least two meaningful units into a phrase			
Non-compositional expression, for example, idiomatic expression [2]	Meaning of the phrase cannot be derived from the parts; full combination needs to be learned to understand the meaning	kick + the + bucket = 'die'	Pyow-hack sequences of putty-nosed monkey [50][a]; possibly 'boom krak-oo', 'boom krak-oo hok-oo' sequence of Campbell monkey [47][b]
Syntax-free compositional expression	Combination of all elements help understanding the meaning; contextual cues important; no grammatical or pragmatic rules	Downtown, movie, fun = 'let's go downtown to see a movie'[c] [51]	Hypothetical example where 'attack, hawk' or 'hawk attack' both mean 'hawk attack'
Compositional syntactic expression, see also [2]	Meaning of the phrase is a function of the meaning of the elements and the way in which they are combined	come + here = 'come here'	ABC–D calls of Japanese tits [8••,20••]; see Figure 1

[a] It has been suggested that pyow-hack sequences also could reflect sequences with a weak literal meaning where an urgency principle helps in their interpretation, that is, the first call is more important than the second one [25•].
[b] Additional experiments are required to assess whether these sequences are indeed idiomatic, or whether they are compositional.
[c] Expressions of children using sign language without having learned a full developed sign language; 'downtown, movie, fun' are in all 6 permutations judged equally [51], but have a clear compositional element.

they are given in much wider array of contexts than songs, such as during foraging, group movements or predator encounters [14–17]. In some species, acoustically distinct calls are produced in different contexts and elicit context-specific responses in receivers [7,14]. Thus, bird calls provide an ideal system to study the evolution of features that are analogue to compositional syntax in languages (referred to as compositional syntax hereafter; Table 1).

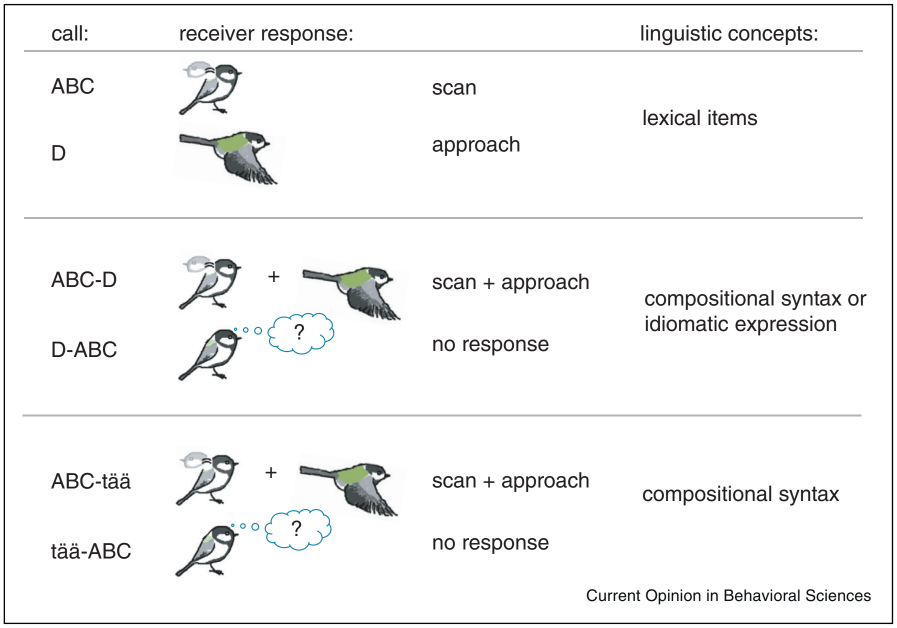
Compositional syntax in birds

It is difficult to know how widespread compositional syntax occurs in birds. Currently, this feature has been explored experimentally only in two species, Japanese tits *Parus minor* and Southern pied babblers *Turdoides bicolor*. Clearly, understanding the meaning of call combinations requires in-depth studies involving detailed experiments to assess their function and meaning, which so far still are rare in birds [18].

Japanese tits occur in forests of Japan, and live in pairs during the breeding season but join mixed-species flocks outside the breeding season that also can include willow tits *Poecile montanus*. Experiments showed that Japanese tits have at least 11 different call elements, which can occur in more than 170 different call combinations [19]. Experimental work focussed on ABC calls (alert calls; Figure 1), D calls (recruitment calls) and ABC–D call combinations given when mobbing a stationary predator [20••]. ABC calls elicit scanning, D calls elicit approaching, while ABC–D calls cause receivers to approach the sound source, intermittently perching to scan as they approach, a combined behaviour that individuals never produce in other contexts (Figure 1). However, receivers do not respond to artificially reversed calls (D–ABC), suggesting that they use an ordering rule to decode call combinations [20••]. Experiments where D calls were replaced with a synonymous recruitment calls of willow tits (tää calls) showed that receivers responded only to ABC–tää calls but not to tää–ABC calls [8••]. Moreover, receivers respond to both D and tää notes alone by approaching, but fail to do so when exposed to artificial shortened tää calls with increased similarity to D calls. Finally, receivers neither respond to artificial call combinations where ABC calls are followed by alert calls of willow tits (zi calls; Figure 3). Thus, Japanese tits seem to extract a compound meaning from a combination by assessing and combining the meaning of the component calls, causing receivers to display both behaviours at the same time (Figure 1). These results suggest that Japanese tits have evolved compositional syntax [8••] (also labelled semantically compositionality [2]; see Table 1). Moreover, the similar response to ABC–D and ABC–tää calls suggests that they did evolve a basic level of abstraction.

Southern pied babblers are cooperatively breeding birds that live in open savannah habitats of Southern Africa. Like Japanese tits, they combine alert with recruitment calls during predator mobbing [21••]. Alert calls are given during low-risk situations, for example, a suddenly approaching animal, while recruitment calls

Figure 1



Calls and call combination of Japanese tits, receiver response to these calls and combinations, as well as the corresponding linguistic concepts. ABC: alert call, D: recruitment call, ABC–D natural call sequence given when mobbing a stationary predator, D–ABC artificially reversed call sequence, tää: recruitment call of heterospecific willow tits (synonymous to D calls); see [8••,20••].

are given when moving to facilitate group cohesion. Experiments showed that sequences where the alert call is followed by a recruitment call causes receivers to approach while being alert, but receivers did not change their behaviour in response to call sequences where alert calls were replaced with foraging calls [21••]. Babblers might interpret alert-recruitment call combinations as semantically compositional expression (see Table 1) or as non-compositional expression (i.e. idiomatic expression). Thus, additional experiments would be required to differentiate between these options. Interestingly, recruitment calls evoke a higher vigilance response than alert calls [21••], suggesting that babblers may perceive the individual calls and their combinations as warning signals that convey a different degree of threat, for example, by predators or conspecifics.

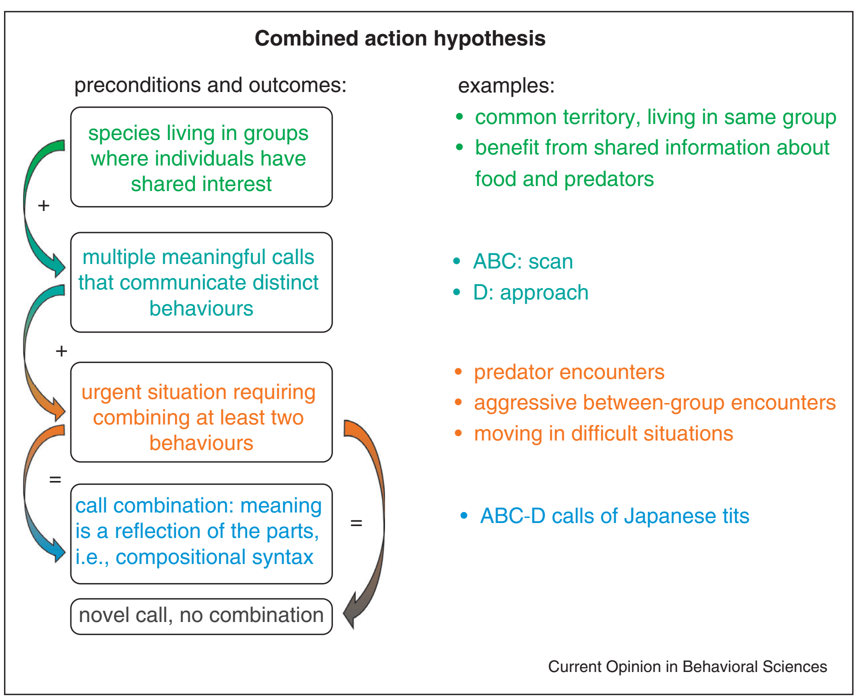
Despite that Japanese tits and pied babblers belong to taxonomically distant songbird lineages, their call combinations involve alert calls followed by recruitment calls, suggesting that the order of the call elements follows an urgency rule where the more urgent alert call is given before the less urgent recruitment call. Urgency-based call ordering has been shown also in mobbing calls of Carolina chickadees *Poecile carolinensis* [22], warning calls of Richardson's ground squirrel *Spermophilus richardsonii* [23] and Campbell's monkeys *Cercopithecus campbelli* [24], and possibly call combinations of putty-nosed monkey *Cercopithecus nictitans* [25•].

What favours the evolution of compositional syntax?

Several hypotheses have been proposed to explain language evolution in a broad sense, and thus, may also explain the evolution of compositional syntax: the universal grammar hypothesis [26], the courtship hypothesis [27,28], the gossip hypothesis [29], the social cognition hypothesis [30], kin selection hypothesis [31] and the information donation hypothesis [32]. The universal grammar hypothesis proposes that syntactic rules evolved before language as a cognitive tool outside the domain of communication [26]. While this hypothesis is disputed [2], the idea that language features evolved before language is widely supported [1•,2]. The courtship hypothesis was first proposed by Darwin, suggesting that language could have evolved from a form of courtship song where different call elements were combined but the meaning of the song was not derived from the meaning of the notes ([27], see also [28]). However, this cannot explain why compositional syntax should evolve since the meaning of song sequence is not a reflection of the meaning of the parts, as the case in languages or Japanese tit ABC–D calls. The gossip hypothesis suggests that language evolved as a means to facilitate the social relationships within a group [29]. While gossip is undeniably an important aspect of language, it seems unlikely for language to evolve merely as a feature to increase social bonds through gossip instead of sharing useful information. Thus, it seems not suited to explain the evolution of compositional syntax. The social cognition hypothesis proposes that the elaborated social interactions in primates facilitated the evolution of discrete combinatorial abilities in social contexts [30], which subsequently provided an essential building block of human language. Clearly, elaborated social interactions alone are not sufficient for the evolution of compositional signals, which otherwise would be found quite widespread [2]. Alternatively, it has been argued that kin selection did play a role for language evolution [31], as a high relatedness between sender and receiver reduces the costs of sharing information. Kinship can increase the willingness of individuals to share information, for example, warning calls can be specifically aimed at kin in several species [33–36] to boost their survival [37]. Accordingly, compositional syntax should evolve particularly in family living species [38], but Japanese tits do not live in family groups [38], making it an unlikely explanation for the evolution of compositional syntax. Finally, the information donation hypothesis suggests that language evolved after human ancestors evolved cooperative breeding and hunting [32]. This setting facilitated the evolution of a prosocial psychology that involves sharing of food, skills and information [39], and therefore also could favour the evolution of compositional syntax. Clearly, any species that forms stable social bonds with other individuals and have a certain level of shared interest [40] should be interested in sharing information with social partners (see below). On the basis of this idea and the so far sparse information on the occurrence of compositional syntax, we propose the combined action hypothesis (Figure 2).

We hypothesize that compositional syntax should evolve in species where individuals firstly, evolved a certain level of shared interest; secondly, evolved multiple meaningful calls; and finally, have a need to communicate combined messages that require receivers to exhibit two behaviours together (Figure 2). An important but often overlooked precondition for many social behaviours is a certain degree of shared interests [40], which facilitates a prosocial psychology and sharing resources and information [1•]. Shared interests can arise when individuals contribute to a common resource, such as reproduction, territory defence, food acquisition or predator protection [40]. A breeding pair has to coordinate its activities and share information about predatory threats to breed successfully [41]. Similarly, individuals in a group benefit from shared information about food and predators [17,42]. A good number of bird species have evolved a range of distinct calls to communicate this information, for example, contact calls to maintain group cohesion [8••] or locate their group after losing contact [17], recruitment calls to attract conspecific and heterospecifics to food [6], or warning calls to share specific information about predators [14,43].

Figure 2

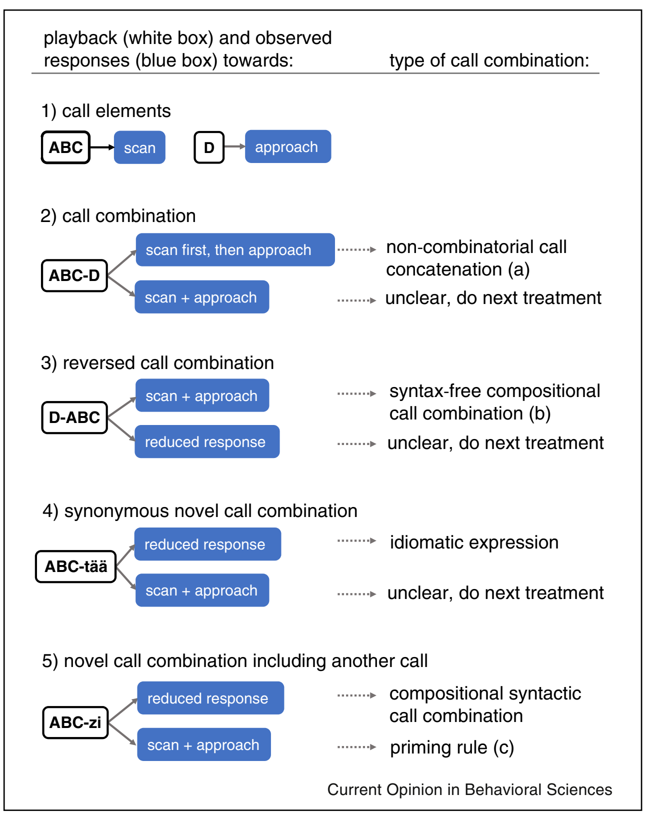


Combined action hypothesis aiming at explaining the evolution of compositional syntax. This feature is proposed to evolve in species where individuals have a certain level of shared interests [40] (making information sharing adaptive), that have evolved multiple meaningful calls and are exposed to urgent situations that require the display of multiple behaviours. Instead of compositional syntax, species could evolve a novel call to communicate the combined message, although this is likely to come at a cognitive cost [3].

Several of these calls have been shown to be functionally referential [7,14,20••], allowing receivers to respond appropriately, for example, displaying appropriate behaviours during predator encounters [14]. In some of these contexts, individuals communicate multiple messages in a call sequence (e.g. alert calls and recruitment calls as the case in Japanese tits and pied babblers), causing receivers to display two behaviours together [8••,20••,21••]. Particularly in risky situations, communication should be clear and as detailed as required to display an appropriate response, which could facilitate the evolution of compositional syntax. Detailed experiments that assess the meaning and function of calls and their combinations are required to distinguish how recipients perceive these call combinations (see Table 1 and Figure 3).

These preconditions occur widespread in birds and mammals, suggesting that additional preconditions are required for the evolution of compositional syntax, or that it occurs more widespread than currently assumed. Notably, these preconditions were also present in human ancestors, which lived in social groups as nomadic hunters-gatherers [44], where individuals benefited from exchanging information about food, predators and social interactions with other group members. Moving into more open savannah habitats increased the exposure to predators and conspecific groups, and thus, the need for efficient predator avoidance and coordination of group movements and different tasks during hunting and when encountering hostile groups of conspecifics [1•]. Our ancestors may have responded to these selective pressures by evolving compositional syntax. Once this ability did evolve, it provided the opportunity to be used in different contexts, expanding the expressive power tremendously, and boosting cognitive evolution [45].

Figure 3



Flowchart of a possible experimental methodology to assess the linguistic nature of a call combination, exemplified with the call combination of Japanese tits. Note that the some of the 'observed receiver response' are hypothetical to illustrate the different possible outcomes. See also Table 1 in [18]. tää and zi calls: recruitment and alert calls of heterospecific willow tits. Reduced response: receiver exhibit some scanning and approaching but to a much lower degree than in response to ABC–D calls. **(a)** Non-combinatorial response, sequential response reflecting call order. **(b)** All combinations including ABC and D elicit scan + approach. **(c)** All combinations starting with ABC elicit scan + approach.

Conclusions

Compositional syntax is a critical feature of language that independently evolved in at least one bird lineage [8••] and potentially in two mammalian lineages [46,47]. Besides Japanese tits, however, further experiments are required to assess whether recipients of these species interpret these call combinations as idiomatic non-compositional or semantically compositional expressions (see Figure 3). Future work can give insights on the evolutionary trajectories leading towards combinatorial abilities and other language-like features. The experiments in Japanese tits indicate that they did evolve an abstract rule system, allowing them to understand truly novel call combinations [8••], but it remains open if tits can use this ability in other contexts. Moreover, it remains unclear whether the cognitive abilities underlying combinatorial abilities evolved in consort with them, or before, as, for example, proposed by the social cognition hypothesis [30]. Interestingly, Japanese tits and pied babblers use meaningful call combinations when mobbing predators. Mobbing is not a high-risk situation where receivers immediately seek safety to avoid predation [37], but rather a behaviour that involves displaying multiple behaviours together, aiming at moving on the predator [48]. More generally, in situations where callers and receivers have a certain level of shared interest [40] and communication should be clear and as detailed as required to display an appropriate response that involves multiple behaviours together, compositional syntax may evolve. Future detailed experimental studies in additional avian and mammalian lineages will allow us to test this hypothesis and explore the social and ecological drivers of compositional syntax.

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Conflict of interest statement

Nothing declared.

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