Review

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Language evolution in the laboratory

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The historical origins of natural language cannot be observed directly. We can, however, study systems that support language and we can also develop models that explore the plausibility of different hypotheses about how language emerged. More recently, evolutionary linguists have begun to conduct language evolution experiments in the laboratory, where the emergence of new languages used by human participants can be observed directly. This enables researchers to study both the cognitive capacities necessary for language and the ways in which languages themselves emerge. One theme that runs through this work is how individual-level behaviours result in population-level linguistic phenomena. A central challenge for the future will be to explore how different forms of information transmission affect this process.

The problems of language evolution

How did language evolve? A complete answer to this question requires that we describe both the biological evolution of the various cognitive mechanisms necessary for language and the cultural evolution of languages themselves (Box 1). Both parts of this effort are limited by the lack of direct natural data on genuine emergence. There is, however, some indirect evidence on which evolutionary linguists can and do draw. With regard to biological evolution, we can explore to what degree the cognitive foundations of language are shared with other species [1,2]. With regard to cultural evolution, we can look at various sources of natural data, such as the emergence of new sign languages [3]. However, these endeavours are inevitably constrained by the fact that only limited experimental control can be exercised. Given this, another historically popular methodology has been to use computer simulations to model and test the effects of various processes and scenarios that are hypothesised to be of importance (Box 2). This project has been reasonably successful [4,5], but no model can hope to replicate all aspects of the evolution of language.

In recent years a new approach has emerged: the development of experimental approaches that use human participants to observe the emergence of symbolic communication systems. The earliest stages of this development have been reviewed [6], but since then several more studies have been published, some of which [7–10] have been explicitly based on and/or inspired by previous computational work. This development raises a number of questions: how do these various studies relate to earlier computational work and to other approaches to language

evolution? How do they relate to each other? What do they tell us about language evolution?

This review attempts to answer these questions. The next section considers how signals are created in the first place. We then look at how communication systems emerge and the impact that interaction and cultural transmission have on the system. Throughout, we seek to relate these findings to other research on language origins. The main papers that we consider are listed in Table 1. A common theme that arises from these studies is that the linguistic phenomena that emerge cannot be explained only by reference to individual cognition. The various forms of interaction that individuals engage in (cultural transmission, feedback, etc.) are observed to be explanatorily important. Consequently, repeated individual-level behaviours result in population-level linguistic phenomena, as Darwinian population thinking would predict [11,12].

Signal creation

In one computational study (Box 2) [13], pairs of robots evolved a communication system without a pre-established communication channel. This novelty highlighted an important conceptual point: before we can concern ourselves with the question of how meanings emerge, there is an initial problem of how organisms (or computational agents) recognise that certain behaviours are indeed communicative in nature [14]. Recent experimental work has sought to explore how pairs of human participants do this in the absence of an already established system. The embodied communication game (ECG) [7] is a two-player game designed to explore this question. To achieve success, participants must solve a coordination problem, which requires both that they travel around a simple 2×2 grid and that they communicate with one another. However, they only have one behaviour they can perform: movement. Thus, they must find a way to reveal to the other player the fact that a given movement, or set of movements, is

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Glossary

Compositionality: key design feature of language whereby the meaning of an expression is a function of the meanings of its constituent parts and the way in which they are combined.

Homonymy: relation between words that have the same form but different meanings (e.g. a writing implement; a small enclosure for animals; a female swan); common in natural languages, such as pen in English.

Iterated learning: process in which the behaviour of one individual is the product of observation of similar behaviour in another individual who acquired the behaviour in the same way (Box 3).

Protolanguage: term used to refer to hypothesised early or earliest form of language, when it did not yet exhibit the full range of structural properties that modern language does.

Systematicity: key design feature of language whereby a feature that is common to more than one item is represented in the same way for each different item; these component parts can then be reused in novel combinations, such as morphemes in natural language.

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Box 1. Language evolution

Research into both how and why language evolved is necessarily highly diverse. It draws on expertise and data from an unusually wide range of disciplines, from genetics to anthropology and from linguistics to evolutionary biology. Other reviews [44] have surveyed the interdisciplinary nature of the field and highlight the multitude of questions that arise and the techniques brought to bear on these questions. Rather than repeating these points, we focus here on an interesting ambiguity inherent in the term language evolution, one that highlights an important conceptual distinction of particular importance to the experimental approaches reviewed here.

The term evolution can be understood in a wide sense as simply change over time. If so, then the evolution of language might refer both to the biological process whereby the capacity for language arose in our species [45] and the ongoing historical process of language change [46]. However, a narrower concept characterises the field more accurately. Language evolution researchers are interested in the processes that led to a qualitative change from a non-linguistic state to a linguistic one. In other words, language evolution is concerned with the emergence of language (Figure I).

Some ambiguity deliberately remains. We do not specify whether this is a biological process (in which our faculty for language emerged through genetic changes) or a cultural one (in which language arose over time through a series of interactions between individuals). A central message of this review is that these two processes should not be considered in isolation. Biology equips individuals with particular cognitive adaptations that have implications for the way social interaction and social learning operate to produce linguistic phenomena. Individuals do not construct languages alone. We need to consider exactly how individuals interacting in dynamic structured populations can cause language to emerge.

Once we have a better general understanding of the mechanisms of social coordination and cultural evolution, gained from the type of experimental work reviewed here, then we can combine this with models of biological evolution to gain a more complete understanding of the evolution of language. The latter without the former will inevitably give a distorted picture of the biological prerequisites for language.
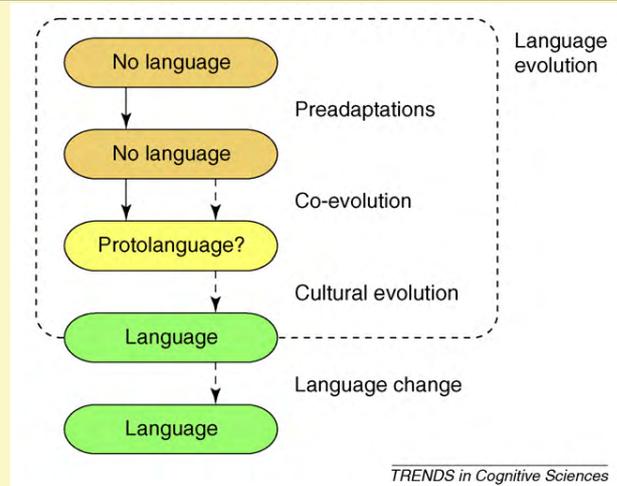

Figure I. Aspects of language evolution. We can characterise the study of language evolution as being concerned with the emergence of language out of non-language. This involves two main processes of information transmission and change: a biological one (shown here with solid arrows) and cultural one (shown here with dashed arrows). Prior to the existence of a culturally transmitted communication system, we can consider only the various preadaptations for language (e.g. vocal learning, conceptual structure; [47]). Once cultural transmission is in place, then it might operate simultaneously with biological evolution in a co-evolutionary process and/or there might be cultural evolution alone [48]. In either case, we urgently need a better general understanding of how cultural transmission and social coordination shape language if we are to achieve a complete picture of the evolution of language. Once language has emerged, further changes can and do occur. This is the domain of language change and historical linguistics.

communicative in nature rather than an act of travel. This is remarkably difficult and many pairs fail altogether. Those that succeed do so usually because they find a way to establish some common expectations of each others' behaviour, and they then use salient deviations from these expectations to make manifest that a given behaviour is intended to be communicative. This shows that common ground, which is known to be important in everyday linguistic communication [15], is also important, and arguably even more so, in the emergence of such communication.

Box 2. Impact of computational models on experimental approaches to language emergence

There is a rich history of computational models of language evolution, with a wide range of diversity in methodological approach and in the types of questions the models seek to address [4,5]. Some of the experimental studies reviewed in this article were directly inspired by previous models. More generally, it is possible to observe deep commonalities between some computational and experimental approaches, even if the former are not explicitly cited as an inspiration for the latter. For example, the earliest experimental work reviewed here [21] has much in common with the Talking Heads research project [49], in which populations of robots negotiated the form that a communication system will take.

We point to three specific examples in which the computational literature has been explicitly cited as a direct influence on the creation of experimental approaches. The first is an intriguing piece of research [13] in which pairs of simulated robots, equipped only with motors and sensors for detecting obstacles, were placed in the centre of an environment and were evolved according to their ability to travel in the same direction as each other. A communication system emerged in which the robots oscillated back and forth to indicate a proposed direction of travel. The key conceptual point here is that initially there was no *a priori* distinction between communicative and non-communicative behaviour, and thus for communication to evolve, there must

be some process by which non-communicative behaviour takes on a communicative role. A number of the studies reviewed here [7,16,18] investigated how human participants achieve this, and one [7] made explicit use of the abstract structure of this study.

The second example is the various simulations that have explored how social behaviour can influence the emergence of linguistic diversity. Although some models [50,51] showed that high linguistic diversity can arise simply as a result of variation in the frequency at which agents interact, others [52,53] showed that a pressure to select linguistic variants on a social basis can increase both the amount of diversity and its stability. This is also the conclusion of subsequent experimental approaches to the emergence of linguistic diversity [8,9], the structure of which was directly influenced by previous computational studies (especially [53]).

The third example is the impact of iterated learning, and vertical cultural transmission in particular, on linguistic structure (Box 3). This has been extensively explored in the computational literature and consequently had a direct influence on at least two of the studies reviewed here [10,25], which were specifically designed to mirror the structure of previous computational work [38]. Iterated learning has also influenced cultural evolution experiments in other domains, particularly for non-humans [39].

Table 1. Differences and similarities between experiments on the emergence of language[a]

Study	Dynamics	Meanings	Forms	Familiarity	Embodiment	Classification proposed in [43]
[18]	Closed group (dyad)	Pre-specified, unstructured	Discrete	None	Yes	Coordination semiotic
[28]	Closed group (community)	Pre-specified, unstructured	Analogue	Indirect	No	Referential semiotic
[29]	Closed group (community) and closed group (dyad)	Pre-specified, unstructured	Analogue	Indirect	No	Referential semiotic
[21]	Closed group (dyad)	Open-ended	Analogue	None	No	Coordination semiotic
[26]	Closed group (dyad)	Pre-specified, unstructured	Analogue	Indirect	No	Referential semiotic
[27]	Linear transmission and closed group (dyad)	Pre-specified, unstructured	Analogue	Indirect	No	Referential semiotic
[32]	Linear transmission	Pre-specified, structured	Discrete	Yes	No	Referential linguistic
[7]	Closed group (dyad)	Open-ended	Discrete	None	Yes	Coordination semiotic
[24]	Closed group (dyad)	Pre-specified, structured	Discrete	Yes	No	Referential linguistic
[25]	Closed group (dyad)	Pre-specified, structured	Analogue	Indirect	No	Referential semiotic

[a]Dynamics refers to the interactions that determine the system. We distinguish between closed groups, linear transmission and replacement (Box 3). The space of meanings that signals refer to can be prespecified or left open-ended. Meaning spaces that are prespecified can be structured or unstructured (e.g. a set of meanings that includes fireman, fire station, policeman and police station is structured, but a set that includes fireman, police station, haystack and tree is not). The forms used to refer to these meanings can be either discrete or analogue. Familiarity asks where participants are asked to use entirely novel signals or not. The various Pictionary tasks are classified as indirect because although the signals used are novel, they often build on conventional depictions. Embodiment is about whether there is an *a priori* difference between communicative and non-communicative behaviour. Studies that are embodied make no such distinction. The obvious way in which there would be a difference is if the communication channel is predefined, but this is not the only way. Finally, the column on classification adopts the distinction, proposed elsewhere [43], between referential semiotic games (in which participants graphically describe a referent without letters, numbers or other standard signs), coordination semiotic games (in which participants have to agree not only on the forms used for each referent, but also on what those referents are) and referential linguistic games (in which participants develop communication systems that exhibit features of linguistic interest).

Related work leads to a similar conclusion. In the tacit communication game (TCG) [16–18], participants must communicate the location and orientation of an object in a 3×3 grid. The TCG shares many important features with the ECG. Indeed, the two games are designed to address the same basic question: the communication and recognition of communicative intent. One difference is that in the TCG one player is assigned the role of sender and one the role of receiver. The receiver is primed to interpret the sender's behaviour in communicative terms, and the sender knows as much. These expectations seem to facilitate the recognition of communicative intent, just as mutual expectations of behaviour in the ECG provide the common ground that allows communicative behaviour to be disambiguated from non-communicative behaviour.

The challenge posed by these games is how participants can communicate their communicative intent. Thus, the games attempt to explore precisely what cognitive capacities are necessary for linguistic communication and how those capacities influence signal form – it is often the case that the final form that signals take is influenced by the fact that the signal had to communicate communicative intent [7]. Thus, if we are to understand the origins of language, we must uncover the cognitive mechanisms that enable us to communicate and detect communication intentions, and seek to understand how this influences signal form. This is a central question for future research, not only because it has important implications for language evolution research [2,19], but also because it is of general theoretical interest for pragmatics, psycholinguistics and other related disciplines [20].

The emergence of communication systems

Once communicative intent is recognised, how do pairs or groups of interacting individuals negotiate on the form and meaning of signals? In one pioneering approach [21], pairs of participants were asked to communicate with each other to solve a coordination problem, but to do so they had to invent and agree on a new set of signs to use. In addition to its relevance to language evolution, this work illustrates how human communication can be understood as a form of joint action [22,23]. Moreover, because it demonstrated that the emergence of such a system could be observed in the laboratory, this work served as inspiration for many of the studies that followed. For example, it inspired a study in which participants were given fixed, finite sets of meanings and symbols, but had to negotiate the mappings between these sets [24]. The study went on to demonstrate the utility of compositionality: when the set of meanings to be communicated is changeable, pairs of participants that have established compositional communication systems fare better than those that have developed holistic systems.

A particularly productive subsequent line of research on the role of interaction in the emergence of communication systems has been the use of graphical communication tasks [25–29]. One advantage of graphical communication is that it provides a medium in which new signs can be invented and used in an interactive context with relative ease. Moreover, previous psycholinguistic work has demonstrated that with there are important similarities between graphical and verbal communication with respect to the effects of interaction on signal form [30]. This suggests that conclusions obtained in one medium will transfer to the other.

The basic approach of graphical communication experiments has been to make use of Pictionary-style games, in which one participant must draw and the other guess the intended referent (Figure 1). A headline result is the importance of direct interaction in the evolution of a learned symbolic communication system out of an initially iconic one. Feedback on the success or otherwise of a participant's conversational contribution is a key constraint both for the initial emergence of learned symbolic communication systems [31] and for their subsequent evolution into a qualitatively different form [26]. Similar results emerge for community-based interaction, in which participants are paired with a different member of the
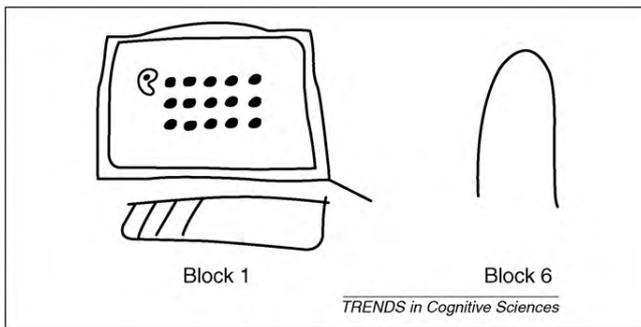
Figure 1. Initial and final drawings for the concept 'computer monitor' from the study by Garrod *et al.* [26] showing evolution of the graphical communication system from iconic to symbolic over time in the experiment. In this experiment, a participant (the director) attempted to represent each of a prespecified list of concepts by drawing on a whiteboard with the aim of getting another participant (the matcher) to correctly identify the target concepts. Over multiple blocks, the roles of director and matcher were repeatedly reversed, but the set of concepts remained the same. This led to evolution of the drawings produced because participants were able to increasingly leverage their interaction history in communicating graphically. In certain conditions, this resulted in the evolution of symbolic representations from initially iconic ones. Reproduced with permission from [26].

community for each interaction [29]. Moreover, if the set of referents to be communicated are conceptually related, then pairwise interaction can lead to the emergence of a characteristic feature of natural languages: systematicity (Figure 2) [25], in which a feature that is common to more than one item is represented in the same way for each different item. This illustrates an important conceptual point that runs through much of this line of research: individual-level behaviours and interactions can give rise to population-level linguistic phenomena. We return to this idea in the conclusion.
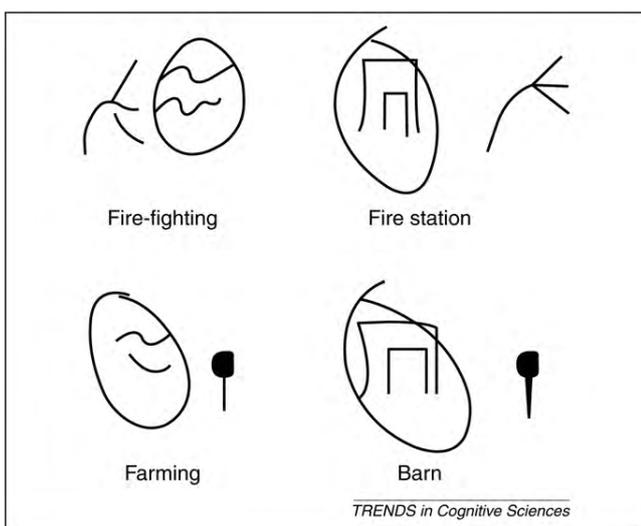

Figure 2. Subset of the final drawings in the experiment of Theisen *et al.* [25] showing how a structured space of meanings can lead to the emergence of compositional structure in the space of signals. In this experiment, meanings were organised according to an underlying two-dimensional grid so, for example, one row of the grid might correspond to concepts relating to farming and one column might correspond to buildings. Participants were not given this grid explicitly, but nevertheless there was very rapid emergence of an internal structure to the signs used. In this example, parallel wavy lines in a circle mean something like 'action' and a line with a blob on top means 'relating to the farm', and so on. Reproduced with permission from [25].

Box 3. The iterated learning model

Iterated learning is 'a process in which an individual acquires a behavior by observing a similar behavior in another individual who acquired it in the same way' [10, p. 10681]. Examples include birdsong, music and language. However, behaviours that involve explicit teaching, such as most sports, are not instances of iterated learning, despite being culturally transmitted.

The iterated learning model (ILM; see [54] for an overview) is an attempt to understand the dynamics that arise from iterated learning and in particular the relationship between the properties of the individual learner and the resulting population-level behaviours. The ILM is often associated with a particular type of vertical cultural transmission, but this is not definitional of iterated learning, which can take place even in horizontal negotiation of conventions between peers. In particular, the graphical communication tasks discussed in the main text [25–29] are instances of iterated learning – it is just that in this case the iterations pass back and forth between the same pair of individuals, rather than along a vertical chain of different individuals.

Computational [33] and mathematical [32,55] ILMs have looked at how basic design features of human language might arise from a subtle interplay between learning bias on the one hand and transmission bottlenecks on the other. In these models, a population of individuals with a particular learning machinery engage in alternating bouts of observable behaviour and learning from that behaviour. A transmission bottleneck exists wherever there is imperfect information about the target of learning. This can arise from factors such as limited training data (i.e. poverty of the stimulus) and transmission noise, among others. In these cases, iterated learning becomes an adaptive system: the behaviour being transmitted changes to optimise transmissibility. Key results in this area include explanation of the origins of compositionality in language [33] and demonstration that in certain conditions cultural transmission can amplify weak learning biases [32].

Cultural evolution

Once a language of some sort has been established, it must be learned anew by each generation. This vertical cultural transmission is an instance of iterated learning, in which the behaviour of one individual is the product of observation of similar behaviour in another individual who acquired that behaviour in the same way [32,33]. Note that whereas iterated learning has often been studied within the context of vertical cultural transmission over multiple generations, this definition makes it clear that iterated learning applies to other forms of interaction as well, including many of those discussed above [33–35]. (Note that although the phrase vertical cultural transmission is often used to refer to the specific case of parent–offspring transmission [36], we use it more generally to refer to cross-generational transmission, regardless of the relation between the individuals.)

Previous modelling work showed that iterated learning has profound effects on linguistic structure (Box 3). This line of research has recently been transferred to the laboratory [10]. Participants were asked to learn a language that consisted of a series of strings of syllables paired with pictures (i.e. meanings). The set of meanings was structured (each item is one of three shapes that takes one of three colours and travels in one of three ways), but the initial strings were not. Participants were tested on their knowledge of this language and their answers were then used as the training data for the next participant. Initially, the languages degenerate, so that after a handful of generations only a small number of distinct words are used and

many aspects of meaning are lost (i.e. there is a lot of homonymy). However, this loss of expressivity is not random. Although meanings are encoded holistically, the words that remain underspecify meanings in structured ways. For example, there might be a single word that means all red things and another that means any bouncing blue thing. It seems, then, that the process of cultural transmission makes languages more learnable because there are far fewer terms to learn, but they lose a great deal of expressive power in the process.

To counteract this, a second experiment was conducted in which all instances of homonymy were filtered out of the training data. Thus, if a participant produced the same word for more than one object, then only one of these was shown to the next participant. The languages became increasingly structured over the generations and began to exhibit compositionality, a key species-unique hallmark of human language [37]. In effect, the languages became both learnable and expressive. Moreover, the study argued that this property is necessarily the consequence of cultural transmission, because it emerged only when the homonymy filter was applied; if compositionality were the result of intentional design on the part of the participants, then it would have emerged in both conditions (especially because participants did not know which condition they were in). Indeed, it was precisely to isolate the effects of cultural transmission that interactive communication and other relevant factors were excluded [38]. These results replicated those found in previous modelling work [34,35] and thus make a compelling case that cultural transmission can turn unstructured languages into structured ones. Similar results have since been demonstrated in the communication system of songbirds [39].

Population dynamics
It could be argued that such experiments in fact show that cultural transmission alone does not produce useable structured languages; instead, it produces degenerate, inexpressive languages. It was only after the languages were filtered for homonymy that compositionality emerged. A system with homonymy is more ambiguous than one without, and thus it seems that in the absence of pressure against homonymy (and indeed against other features that might reduce the utility of a linguistic system) then languages will degenerate.

Communication provides just such a pressure. This point is brought into focus by recent experimental work that contrasted vertical cultural transmission with repeated pairwise interaction [27]. Pictures were correctly guessed more often in the interactive condition than in the cultural transmission condition. Furthermore, the complexity of the drawings (measured by the amount of ink used) decreased over time in the interactive condition, but not in the vertical cultural transmission condition. This coupling of decreasing complexity and increasing accuracy observed in the interaction condition suggests that, over time, drawings in the interactive condition might have taken on a more symbolic nature. This is, after all, what happened in the original work on the emergence of graphical communication systems [26]. In the vertical cultural transmission condition, by contrast, drawings retained an iconic appearance. This suggests that different types of iterated learning (both pairwise interaction and vertical cultural transmission are instances of iterated learning; Box 3) place different pressures on systems. Vertical cultural transmission requires that systems be learnable (by those not involved in its creation), whereas repeated pairwise interactions require that the system be expressive (in the sense that it disambiguates from other possible referents in the most efficient way possible). This conclusion illustrates that a central question for future research must be to establish how different population structures affect the dynamics of evolving communication systems, and how they interact with one another (Figure 3). One specific unanswered question is the relative contributions of interaction (i.e. where participants play with the same partner or set of partners repeatedly) and feedback (i.e. where participants receive information about
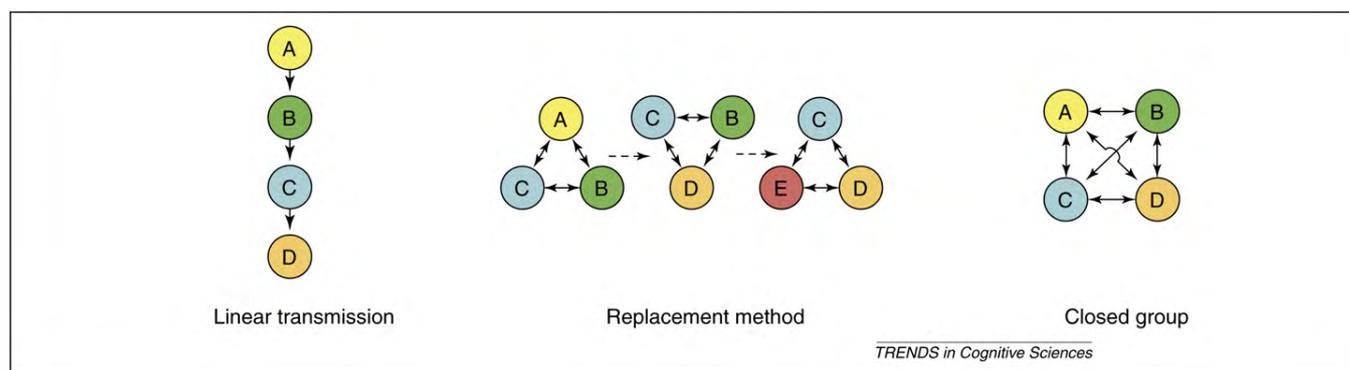

Figure 3. Three different modes of cultural transmission. Mesoudi and Whiten [42] set out a taxonomy of different modes of cultural transmission and we can usefully apply this framework to experiments on the evolution of language. Their fundamental division is between the linear transmission chain method, the replacement method and the closed-group method. In the diagrams above, solid arrows indicate information that is being transmitted culturally (e.g. by iterated learning). The dotted arrows in the middle figure indicate how the population changes over time. The simplest model is the linear transmission chain, in which language is passed from generation to generation purely vertically. Here it is shown with a single individual per generation, but linear transmission can also occur between generations made up of multiple individuals. In the replacement method, members of a population are gradually replaced one-by-one with new members. At each stage, population members learn from the rest of the population, leading to both horizontal and vertical transmission of behaviour. Finally, in the closed-group method, the population is static in the sense that no members are removed or added at any stage. In these cases, we can also imagine structured populations in which there are constraints on which individuals interact (e.g. modelling spatial structure or social networks). The minimum closed-group model is the dyad, in which behaviour is repeatedly transmitted and shaped by iterated learning between two individuals.

whether their partner has understood their message correctly) in the emergence of linguistic phenomena. Until now, these two different aspects have been studied together, but it might be the case that one or the other is driving the results observed so far.

Concluding remarks

This review has highlighted an interesting recent development in research on language origins: the use of laboratory-based experiments on language emergence. We have reviewed several such studies, but these are not the only demonstration of this development. We have not, for example, discussed interesting recent work on the effects of rapidity of fading on linguistic structure [40], on how group membership and the free-rider problem influence language form and linguistic diversity [8,9], or on the neural basis of communicative intentions [16].

One major benefit of the reviewed work is that it brings greater ecological validity than previous computational experiments. For example, experiments that were directly inspired by previous computational work (Box 2) demonstrate where the conclusions that arose from previous work actually transfer to actual human participants. One general pattern that can be observed is that repeated individual-level behaviours can result in population-level phenomena. Much human collective behaviour can in general be understood as an emergent property in this way [41]. What many of the papers reviewed here illustrate is that this might be true in the specific case of language. Studies reviewed here have, for example, demonstrated the emergence of compositionality [10], systematicity [25] and symbolism [21,26]. Moreover, they have also demonstrated that the various different ways in which information can be passed between members of a community (e.g. repeated pairwise interaction, feedback on communicative success, cultural transmission, etc.) affect this process in different ways. Thus, the transmission process has a substantial explanatory role alongside the contributions of individual cognition. This suggests the following conclusion: we cannot construct a simple equation between a cognitive model of the human capacity for language and the linguistic phenomena we wish to explain. The way in which language is transmitted must also be taken into account (Figure 3). Thus, a key research challenge for the future is to further isolate the specific effects of different types of information transmission. Answers to this and other related questions (Box 4) must then be combined with insights from other approaches (computational modelling, comparative methods, data from natural language emergence, etc.) to draw conclusions about how language most probably evolved.

One obvious criticism arises in discussion of experimental approaches: they inevitably use modern humans, but we do not know what humans were like at the point when language emerged. However, the goal of experimental approaches is not to replicate the evolutionary history of language. Rather, these experiments enable us to investigate the precise nature of the various phenomena (both biological and, especially, cultural) that underpin the emergence of shared symbolic communication systems. The results of all the above experiments are testimony

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> **Box 4. Questions for future research**
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> - What are the prerequisites for recognition of communicative intent?
> - More generally, what cognitive mechanisms are necessary for inferential communication, and how did they evolve?
> - Do the results obtained so far scale up to larger populations with more complex dynamics?
> - Do different population structures influence the way in which language is transmitted? If so, how, and how does this affect linguistic structure?
> - How do experimental studies in the laboratory relate to studies of language emergence in real human populations?
> - What is the relative contribution of feedback, interaction and cultural inheritance (and indeed other forms of information transmission) to the form of the final communication system?
> - Can the results from experimental approaches be used to develop better computational models of language evolution?

to the fact that this task is not impossible and that true insights into the origins of language can be generated with experimental approaches. However, this project remains in its infancy and there is much terrain that remains unexplored.

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