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Iterated learning and the evolution of language

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Iterated learning describes the process whereby an individual learns their behaviour by exposure to another individual's behaviour, who themselves learnt it in the same way. It can be seen as a key mechanism of cultural evolution. We review various methods for understanding how behaviour is shaped by the iterated learning process: computational agent-based simulations; mathematical modelling; and laboratory experiments in humans and non-human animals. We show how this framework has been used to explain the origins of structure in language, and argue that cultural evolution must be considered alongside biological evolution in explanations of language origins.

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Introduction: can culture explain structure?

Language exhibits striking structural design features that mark it out as extremely unusual among communication systems in nature. In particular, utterances in a language are constructed out of sub-parts — phonemes, morphemes, words, phrases — that are reused and recombined in systematic ways. Because of the apparent uniqueness of this design, and because it enables the open-ended expressive potential of human language, linguistic structure has been a primary target for explanation by evolutionary linguists and cognitive science more generally [1–3].

In addition to exhibiting structure, language is one of a rare set of behaviours that persists through a particular kind of cultural transmission: *iterated learning* [4••].

Iterated learning: The process by which a behaviour arises in one individual through induction on the basis of observations of behaviour in another individual *who acquired that behaviour in the same way*.

For example, we induce the particular properties of our language by being exposed to the linguistic behaviour of other individuals in our speech community. Our resulting language in turn leads to linguistic behaviour that shapes the language of further individuals, leading to the possibility of cultural evolution by a process of repeated induction and production of behaviour. In this paper we survey simulations, mathematical models and experiments all pointing towards the same underlying hypothesis: that the key structural design features of language have their explanation in the fact that language is culturally transmitted in this way [4••,5–7]. The rarity of this kind of design in natural communication may appear to be explained as a consequence of the rarity of iterated learning. However, as we will argue at the end of this review, the vocal productions of some other species — most notably, songbirds [8••] — also evolves culturally via iterated learning. This opens up an intriguing avenue for comparative study, and also raises important questions about the differences in the design features of song and language.

Agent-based simulation

Foundational work by Hurford [9] sparked interest in computational simulation as a tool for modelling the biological and cultural evolution of language. Following Hurford's lead, the earliest work in this area sought to explain the role of interaction and negotiation [10•, 11] or biases of learners [12,13] in shaping communication systems, focusing in particular on the conditions under which communicatively optimal, socially learnt communication systems would emerge. Subsequent efforts were directed towards an explanation of how linguistic structure can arise as a consequence of iterated learning. While interaction and learning bias play a role in this process [14,15], much of this work emphasises the role of the *learning bottleneck* [4••,15–19] in driving the evolution of structure: language learners must attempt to learn a large or infinitely expressive linguistic system on the basis of a relatively small set of linguistic data. A key finding is that *compositional* languages (in which the meaning of a complex expression is composed of the meanings of parts of that expression) emerge from holistic (i.e. unstructured) languages as a result of repeated transmission through the learning bottleneck: language structure appears as an adaptive response *by language itself* to the problem of being transmitted through a narrow bottleneck, since the presence of compositional rules enables a learner to infer from a small sample rules underpinning the entire language.

Another rich seam of modelling work looks at the emergence of systematicity in phonological systems through communicative interaction and iterated learning. For example, De Boer [20,21] looks at the cultural evolution of vowel systems, demonstrating that universal features of the organisation of vowels in the world's languages can arise through repeated interaction between simulated agents under certain reasonable articulatory and perceptual constraints. Models by Oudeyer [22,23], Wedel [24,25•], and Zuidema and De Boer [26], despite very different underlying assumptions about the cognitive machinery involved, show that the process of repeated learning and use of a sound system can lead to the emergence of systematic organisation of *sequences* of sounds, as well as the organisation of those sounds themselves in acoustic/articulatory space.

This wide range of agent-based models suggest that key design features of language emerge from iterated learning. Furthermore, the models employed by these authors differ hugely in their approach (they include connectionist models [27], exemplar models [28], grounded robotic models [14], and induction of formal symbolic grammars [18]), suggesting general principles at play in iterated learning that transcend the particular model implementation.

Mathematical models

The insights offered by agent-based simulations of iterated learning have recently been supplemented by mathematical results that characterise how languages can change through cultural transmission. Mathematical modelling has been an important part of the theoretical development of evolutionary biology, and some of the tools that have been developed for analysing biological evolution prove equally powerful for analysing cultural evolution.

The potential of these mathematical tools was demonstrated in a series of papers by Nowak and colleagues [29•,30–32], who showed how one of the basic models of biological evolution — the replicator dynamics — could be modified to capture aspects of language evolution. The replicator dynamics indicates how the composition of a population of different types of organisms, each with a different biological fitness, will change over time. By modifying this model to allow the fitness of each type to depend on the composition of the population, and for offspring to be of a different type from their parents, Nowak and colleagues were able to capture two important aspects of language evolution: the success of a language depends on how many people understand that language, and children can end up speaking different languages from their parents. This framework can be used to rigorously answer questions about, for instance, how constrained language learning needs to be in order to guarantee that a population will end up speaking the same language, and to what extent this *coherence threshold* can drive the evolution of an ever-more restrictive language faculty [29•].

Perhaps as a consequence of their origins in biological evolution, these models made very weak assumptions about the transmission process itself: no language is easier or harder for learners to acquire than any other. As a consequence, the driving force in the dynamics was the effect of fitness — of being able to communicate effectively with others — rather than learning. To explore the effects of transmission more directly, Griffiths and Kalish [33••] developed the first mathematical characterisation of the results of iterated learning, based on analysing vertical transmission chains where each learner acquires a language from the previous learner then generates the data from which the next learner learns. A richer characterisation of learning was provided by assuming that learners follow the principles of Bayesian inference, combining their own biases with the observed data (the linguistic behaviour of others) when inferring a language. These biases, which capture the innate or acquired dispositions that make one language easier to learn than another, are expressed in a *prior distribution* over languages — a probability distribution where languages that are easier to learn are assigned higher probability.

Griffiths and Kalish assumed that each learner made an inference by computing a *posterior* distribution over hypotheses that combined the biases reflected in the prior distribution with the information available in the linguistic data they had encountered. Each agent would then choose a hypothesis by sampling from this distribution, and use this hypothesis to generate data for the next agent in a chain of transmission. Under these assumptions, the hypotheses selected by the agents converge to a particular distribution as iterated learning proceeds: after enough episodes of transmission have passed, the probability that a learner selects a particular hypothesis is just the prior probability of that hypothesis, regardless of where the process of iterated learning started.

This *convergence to the prior* illustrates the potential power of cultural transmission as an evolutionary force: even in the absence of communicative interaction, iterated learning can significantly change the languages spoken by a population. In particular, it can induce a shift towards languages that are consistent with the biases of learners, with those languages that are easiest to learn becoming more prevalent in the population.

While this mathematical characterisation of iterated learning shares some of the conclusions of the agent-based simulation work reviewed above, in particular the emphasis in some of the early work on the role of learner biases in shaping cultural evolution, there are also some important mismatches. First, it indicated that there should be a one-to-one correspondence between the biases of learners and the extent to which a language is likely to emerge through cultural transmission, while simulations had suggested that weak learning biases could be magnified by iterated learning [18]. Second, iterated learning would result in convergence to the same distribution — the prior — regardless of how much data each learner saw. There was thus no effect of the learning bottleneck in the mathematical analysis, in contrast to the important role this seemed to play in simulations.

Attempting to reconcile these differences, Kirby, Dowman, and Griffiths [34] examined the effect of different learning mechanisms on the mathematical results. This analysis showed that the differences from the simulation results were due to the assumption that learners *sampled* a hypothesis from the posterior distribution. If learners adopt a more deterministic strategy — moving towards simply selecting the hypothesis with highest posterior probability — then iterated learning converges to a distribution that exaggerates the prior: hypotheses with high prior probabilities appear even more often, while those with low prior probabilities become even less likely. The exact distribution depends on how much data is seen by each learner, with the prior having a stronger effect when only small amounts of data are available. This analysis thus helps to explain the circumstances under which cultural transmission can magnify learning biases (allowing weak biases to be a potential explanation for strong linguistic patterns) and when a bottleneck effect will emerge. Specifically, it suggests that future empirical work should concentrate on the extent to which acquisition of language appears to involve sampling from a posterior or choosing the hypothesis that maximises the posterior.

Subsequent mathematical analyses have begun to link these results to broader questions about cultural and biological evolution, exploring transmission in more complex populations [35,36], the effects of the structure of the environment on the structure of language [37], formal relationships between iterated learning and the Wright-Fisher model from population genetics [38], and the biological evolution of learner biases [39].

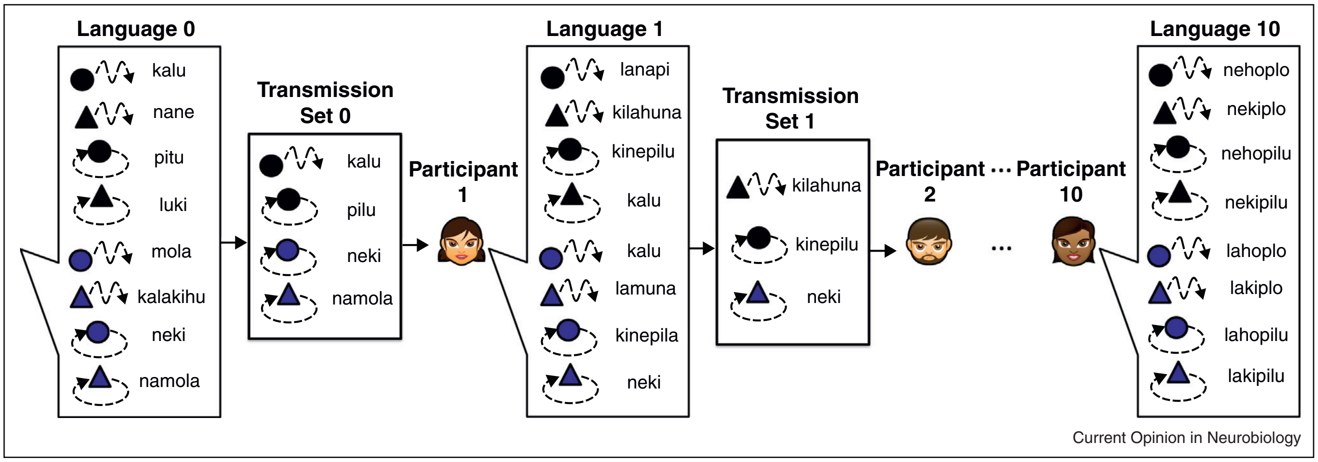
Laboratory experiments

The experimental study of iterated learning goes back at least as far as Bartlett's 'serial reproduction' paradigm [40], in which participants were exposed to some stimulus (e.g. a drawing), then asked to reproduce that material from memory; their reproduced stimuli served as the stimulus for a second participant, and so on. Bartlett observed that material transmitted in this way changed as participants imposed their expectations about the appropriate content onto the recalled material, causing it to be restructured: for instance, drawings might change towards conventional representational forms (see also, [41]). This is an experimental demonstration of the prediction made by the mathematical analysis of iterated learning, outlined above, that systems of knowledge or behaviour transmitted by iterated learning evolve to reflect the biases of individuals involved in transmission.

Much of the modern work using the iterated learning paradigm with humans (see [42] for review) is of a similar nature, demonstrating the presence and consequence of learner biases. Several studies take known biases from well-studied tasks, such as the learning of categories or functions, and verify that transmission through iterated learning yields behaviours which reflect those biases [43,44]; an alternative approach is to use iterated learning as a discovery procedure for biases, for example showing biases in favour of retaining social information over non-social information [45], or using the results of iterated learning to arbitrate between theories of how people make predictions about everyday events [46].

In the domain of language evolution, several studies have combined iterated learning techniques with artificial language learning or communication game paradigms to explore the way in which languages or other communication systems evolve through learning and use (see [48] for review). Kirby and colleagues introduced an iterated learning paradigm (Figure 1) in which participants were trained on an artificial language (a set of labels for coloured moving shapes) and then produced linguistic behaviour which subsequent individuals learnt from [47••] (see also [49]). A learning bottleneck was imposed on transmission: while each participant produced a label for the full set of stimuli, only a subset of those pictures were presented, together with their labels, to the participant at the next generation. From an initial random labelling of objects, the languages changed over generations so as to facilitate generalisation: as predicted by the modelling results discussed above (e.g. [4••]), compositional languages developed, where sub-parts of each complex label specified components of the picture that label referred to (e.g. the first syllable of a complex label might indicate the colour, the second syllable might indicate shape, the third syllable movement). Related experimental paradigms, in which participants learn or communicate using a novel medium (systematically distorted graphical scribbles, or a slide whistle) show the emergence of combinatorial structure, where complex signals are composed by recombining a smaller set of meaningless component parts [50,51,52•], again demonstrating that the predictions of earlier agent-based modelling above are borne out experimentally.

Figure 1



An illustration of the iterated artificial language learning method and indicative results, from [47••]. Data shown is from their Experiment 2, Chain 3. Participants are asked to learn a target language based on exposure to a subset of that language (labelled 'Transmission Set' here), with (a subset of) the language produced by the *n*th participant in a chain of transmission providing the input to participant $n + 1$. In this experiment, participants were asked to learn labels for coloured moving shape (there were 3 shapes, 3 colours, 3 motions: a subset are shown here). The initial language (Language 0) provided a randomly generated, idiosyncratic label for each such picture. As a result of the iterated learning procedure, this unstructured set of meaning-signal associations developed into a structured language: in the chain shown here, by generation 10, each label consists of a prefix specifying colour (e.g. *ne-* for black, *la-* for blue), a stem specifying shape (e.g. *-ho-* for circle, *-ki-* for triangle), and an affix specifying motion (e.g. *-plo* for bouncing, *-pilu* for looping).

The combination of iterated learning and artificial language learning has been used to show that miniature languages exhibiting unpredictable or 'free' variation (largely absent from natural languages) become increasingly regular and predictable as a result of their transmission [53,54], demonstrating that adult learners have a bias in favour of regularity, and that these learning biases can explain the absence of unpredictable variation in natural languages (complementing studies which emphasise the role of strong biases in child learners in imposing regularity on language [55,56]). Using a similar experimental paradigm, [57] demonstrate that miniature vocabularies for describing colour evolve through iterated learning to resemble the distribution of colour naming systems observed in the world's natural languages, again highlighting iterated learning as a mechanism which can explain linguistic universals.

Other work has explored how the nature of interactions between participants engaged in iterated learning can shape an evolving communication system. In an important series of studies [58–61], participants play a graphical communication game in pairs: the *director* produces a drawing which is intended to convey a concept to the *matcher*, who attempts to identify the concept being conveyed by the director. These studies compare simple dyads (two participants play together repeatedly), larger closed groups of eight individuals ('communities'), where members of the group play a series of pairwise communication games, rotating through partners in a controlled fashion, and transmission chains, where drawings were transmitted to naive individuals rather than within closed groups. These three population structures produce different types of graphical communication system. In dyads, participants' drawings develop from rather complex affairs which represent their intended referent iconically (e.g. by resembling the actor or location they depict) to far simpler, economical but opaque symbols, which pick out their intended referent only by convention within the dyad. In contrast, graphical representations in diffusion chains became increasingly complex and iconic. The systems which emerge in communities differ more subtly from those which develop in dyads: community graphical representations are simple, like the representations that develop in dyads, but are less opaque to outsiders and inherently more 'shareable'. Following on from this, other work in the same paradigm further explores the consequences of transmission and interaction for the form and structure of graphical communication systems [62–64].

A range of iterated learning experiments have also been carried out with non-human animals (see [65] for review), being primarily used to establish whether the studied species are capable of faithfully transmitting and maintaining a novel behaviour within a population [66•]. In species where the presence of cultural transmission is uncontroversial (e.g. songbirds), iterated learning has been used as a tool to investigate biases in learning, in close parallel to the experimental work with humans: Feher and colleagues show that an initially degenerate song rapidly reverts to natural, wildtype song as it is passed from tutor to pupil in transmission chains of zebra finches, suggesting that zebra finch learners have strong expectations about appropriate song structure [8••] and, as predicted by the simulation and modelling work reviewed above, these biases shape the evolving song system. In addition to providing a rich toolkit for understanding song, further application of iterated learning as an explanatory framework to learned systems in animal communication, like birdsong, is likely to raise challenging new questions about what makes human language, and humans, special.

Conclusions

We have reviewed over a decade of work using computer simulation, mathematical modelling, and experiments that has shown how iterated learning can produce systematically structured behaviour. We began this review by suggesting that the uniqueness of human language may be due to the unusual way that it is transmitted: the rarity of iterated learning in nature explains the rarity of systematically structured communication systems. In order to test this hypothesis, future research needs to look more closely at the parallels between iterated learning in birds and humans, and the parallels between the structure in birdsong and language. One crucial difference between song and language relates to *meaning*. Language is a culturally transmitted system for mapping between complex signals and complex semantics. The models and experiments showing the emergence of compositionality were based on this observation [4••,47••]. However, there is no evidence that birdsong is semantic in this way. As such, a closer parallel in the human case is the emergence of combinatorial rather than compositional structure [52•].

Finally, we are left with an important unanswered question: how does iterated learning itself evolve? An answer to this question will require further animal studies to understand more precisely the biological prerequisites for this particular type of cultural transmission.

Conflict of interest statement

Nothing declared.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Christiansen MH, Kirby S: **Language evolution: consensus and controversies**. *Trends Cogn Sci* 2003, **7**:300-307.

2. Fitch WT: *The Evolution of Language*. Cambridge University Press; 2010.

3. Hurford JR: *The Origins of Grammar: Language in the Light of Evolution II, vol 2*. Oxford University Press; 2011.

4. •• Kirby S: **Spontaneous evolution of linguistic structure — an iterated learning model of the emergence of regularity and irregularity**. *IEEE Trans Evol Comput* 2001, **5**:102-110.
The first journal paper to present the iterated learning model. This agent-based model shows how compositional structure emerges in a set of signals through a process of iterated learning. It provides a demonstration of the so-called bottleneck effect, whereby smaller amounts of data lead to an increase in the pressure for compositionality. This can explain the oft-noted interaction between frequency and regularity in language.

5. Deacon T: *The Symbolic Species*. London: Penguin; 1997, .

6. Christiansen MH, Chater N: **Language as shaped by the brain**. *Behav Brain Sci* 2008, **31**:489-509.

7. Chater N, Christiansen MH: **Language acquisition meets language evolution**. *Cogn Sci* 2010, **34**:1131-1157.

8. •• Feher O, Wang H, Saar S, Mitra PP, Tchernichovski O: **De novo establishment of wildtype song culture in the zebra finch**. *Nature* 2009, **459**:564-568.
An experimental investigation of iterated learning in bird song. In this paper, we see how the atypical song produced by a Zebra Finch deprived of a tutor can gradually evolve into species-typical song over a small number of generations of iterated learning.

9. Hurford JR: **Biological evolution of the Saussurean sign as a component of the language acquisition device**. *Lingua* 1989, **77**:187-222.

10. • Steels L: *The Talking Heads Experiment*. Laboratorium; 1999.
A detailed account of the talking heads experiments. It sets out the design of an influential approach to modelling the emergence of a shared language through repeated interaction. In the experiment, robotic cameras pointed at a white board covered with coloured shapes are used to ground communication games in a real environment.

11. Steels L: **Evolving grounded communication for robots**. *Trends Cogn Sci* 2003, **7**:308-312.

12. Oliphant M: **The learning barrier: moving from innate to learned systems of communication**. *Adapt Behav* 1999, **7**:371-384.

13. Smith K: **The cultural evolution of communication in a population of neural networks**. *Connect Sci* 2002, **14**:65-84.

14. Vogt P: **The emergence of compositional structures in perceptually grounded language games**. *Artif Intell* 2005, **167**:206-242.

15. Brighton H, Smith K, Kirby S: **Language as an evolutionary system**. *Phys Life Rev* 2005, **2**:177-226.

16. Kirby S: **Syntax without natural selection: how compositionality emerges from vocabulary in a population of learners**. *The Evolutionary Emergence of Language: Social Function and the Origins of Linguistic Form*. 2000:302-323.

17. Kirby S: **Learning, bottlenecks and the evolution of recursive syntax**. *Linguistic Evolution Through Language Acquisition: Formal and Computational Models*. 2002:173-203.

18. Brighton H: **Compositional syntax from cultural transmission**. *Artif Life* 2002, **8**:25-54.

19. Zuidema WH: **How the poverty of the stimulus solves the poverty of the stimulus**. In In *Advances in Neural Information Processing Systems 15 (Proceedings of NIPS'02)*. Edited by Becker S, Thrun S, Obermayer K. *Advances in Neural Information Processing Systems 15 (Proceedings of NIPS'02)* Cambridge, MA: MIT Press; 2003:43-50.

20. De Boer B: **Self-organization in vowel systems**. *J Phon* 2000, **28**:441-465.

21. De Boer B: *The Origins of Vowel Systems*. Oxford University Press; 2001.

22. Oudeyer P-Y: *Self-organization in the Evolution of Speech*. Oxford University Press; 2006.

23. Oudeyer P-Y: **The self-organization of speech sounds**. *J Theor Biol* 2005, **233**:435-449.

24. Wedel AB: **Exemplar models, evolution and language change**. *Linguist Rev* 2006, **23**:247-274.

25. • Wedel AB: **Lexical contrast maintenance and the organization of sublexical contrast systems**. *Lang Cogn* 2012, **4**:319-356.

A simulation showing how cultural transmission can lead to systematic sublexical contrasts. The model in this paper demonstrates that a pressure for simplicity and a pressure for contrast at a lexical level can leads to the spontaneous emergence of systematic organisation of sounds at a sub-lexical level. It provides an elegant abstract explanation for the emergence of phonological systematicity in language.

26. Zuidema W, De Boer B: **The evolution of combinatorial phonology**. *J Phon* 2009, **37**:125-144.

27. Batali J: **Computational simulations of the emergence of grammar**. In *Approaches to the Evolution of Language.* Edited by Hurford JR, Studdert-Kennedy MKC. Cambridge University Press Cambridge: Social and Cognitive Bases; 1998:405-426.

28. Batali J: **The negotiation and acquisition of recursive grammars as a result of competition among exemplars**. In *Linguistic Evolution Through Language Acquisition: Formal and Computational Models.* Edited by Briscoe T. Cambridge University Press; 1999. (Chapter 5).

29. • Nowak MA, Komarova NL, Niyogi P: **Evolution of universal grammar**. *Science* 2001, **291**:114-118.

Using a modified version of the replicator dynamics, Nowak *et al*. establish the existence of a coherence threshold, a minimum level of learning accuracy required for a population to converge on a shared grammar. This coherence threshold depends on the amount of linguistic data learners see, their procedure for learning, and the space of possible grammars they consider. As a result of the coherence threshold, there is selection in favour of a language faculty which reduces the size of the search space to levels that meet the coherence threshold; however, once this threshold has been reached, populations of less constrained learners remain resistant to invasion by even more constrained learners, since some such populations will use languages which more constrained learners cannot acquire.

30. Nowak MA, Komarova NL, Niyogi P: **Computational and evolutionary aspects of language**. *Nature* 2002, **417**:611-617.

31. Komarova NL, Niyogi P, Nowak MA: **The evolutionary dynamics of grammar acquisition**. *J Theor Biol* 2001, **209**:43-59.

32. Nowak MA, Komarova NL: **Towards an evolutionary theory of language**. *Trends Cogn Sci* 2001, **5**:288-295.

33. •• Griffiths TL, Kalish ML: **Language evolution by iterated learning with Bayesian agents**. *Cogn Sci* 2007, **31**:441-480.

A Bayesian framework for investigating iterated learning. This paper provides a general model for deriving the effects of iterated learning with rational learners. It presents an important result showing that iterated learning converges to the prior bias of learners.

34. Kirby S, Dowman M, Griffiths TL: **Innateness and culture in the evolution of language**. *Proc Natl Acad Sci* 2007, **104**:5241-5245.

35. Smith K: **Iterated learning in populations of Bayesian agents**. In *Proceedings of the 31st Annual Conference of the Cognitive Science Society*. 2009:697-702.

36. Burkett D, Griffiths TL: **Iterated learning of multiple languages from multiple teachers**. In In *Proceedings of the 8th International Conference on the Evolution of Language.* Edited by Smith ADM, Schouwstra M, de Boer B, Smith K. *Proceedings of the 8th International Conference on the Evolution of Language* World Scientific; 2010:58-65.

37. Perfors A, Navarro D: **Language evolution can be shaped by the structure of the word**. *Cogn Sci* 2014, **38**:775-793.

38. Reali F, Griffiths TL: **Words as alleles: connecting language evolution with Bayesian learners to models of genetic drift**. *Proc R Soc B: Biol Sci* 2010, **277**:429-436.

39. Smith K, Kirby S: **Cultural evolution: implications for understanding the human language faculty and its evolution**. *Philos Trans R Soc B: Biol Sci* 2008, **363**:3591-3603.

40. Bartlett FC: *Remembering*. Oxford: Macmillan; 1932, .

41. Tamariz M, Kirby S: **Culture: copying, compression and conventionality**. *Cogn Sci* 2014. (in press).

42. Mesoudi A, Whiten A: **The multiple roles of cultural transmission experiments in understanding human cultural evolution**. *Philos Trans R Soc Lond B* 2008, **363**:3489-3501.

43. Kalish ML, Griffiths TL, Lewandowsky S: **Iterated learning: intergenerational knowledge transmission reveals inductive biases**. *Psychon Bull Rev* 2007, **14**:288-294.

44. Griffiths TL, Christian BR, Kalish ML: **Using category structures to test iterated learning as a method for identifying inductive biases**. *Cogn Sci* 2008, **32**:68-107.

45. Mesoudi A, Whiten A, Dunbar R: **A bias for social information in human cultural transmission.**. *Br J Psychol* 2006, **97**:405-423.

46. Lewandowsky S, Griffiths TL, Kalish ML: **The wisdom of individuals: exploring people's knowledge about everyday events using iterated learning**. *Cogn Sci* 2009, **33**:969-998.

47. •• Kirby S, Cornish H, Smith K: **Cumulative cultural evolution in the laboratory: an experimental approach to the origins of structure in human language**. *Proc Natl Acad Sci* 2008, **105**:10681-10686.

The first experimental instantiation of the iterated learning model for a linguistic task. This experiment is closely modelled on previous iterated learning simulations of the emergence of compositionality. Participants learn an artificial language for describing visual stimuli. They are then tested on both seen and unseen stimuli. The resulting labels are then the target language for the next participant. Over time, the languages become more learnable and more structured.

48. Scott-Phillips TC, Kirby S: **Language evolution in the laboratory**. *Trends Cogn Sci* 2010, **14**:411-417.

49. Silvey C, Kirby S, Smith K: **Word meanings evolve to selectively preserve distinctions on salient dimensions**. *Cogn Sci* 2014. (in press).

50. Galantucci B: **An experimental study of the emergence of human communication systems**. *Cogn Sci* 2005, **29**:737-767.

51. Galantucci B, Kroos C, Rhodes T: **The effects of rapidity of fading on communication systems**. *Interact Stud* 2010, **11**:100-111.

52. • Verhoef T: **The origins of duality of patterning in artificial whistled languages**. *Lang Cogn* 2012, **4**:357-380.

An experiment demonstrating how a key design feature of human language — duality of patterning — might emerge from iterated learning. In this experiment, participants learn to copy sets of auditory stimuli using a slide-whistle. The resulting whistle-sets form the training data for the next participant, and so on. Combinatorial structure emerges in the sets of whistles, suggesting a mechanism for the evolution of basic phonological structure in human language.

53. Reali F, Griffiths TL: **The evolution of frequency distributions: relating regularization to inductive biases through iterated learning**. *Cognition* 2009, **111**:317-328.

54. Smith K, Wonnacott E: **Eliminating unpredictable variation through iterated learning**. *Cognition* 2010, **116**:444-449.

55. Hudson Kam CL, Newport EL: **Regularizing unpredictable variation: the roles of adult and child learners in language formation and change**. *Lang Learn Dev* 2005, **1**:151-195.

56. Hudson Kam CL, Newport EL: **Getting it right by getting it wrong: when learners change languages**. *Cogn Psychol* 2009, **59**:30-66.

57. Xu J, Dowman M, Griffiths TL: **Cultural transmission results in convergence towards colour term universals**. *Proc R Soc Lond B* 2013, **280**:20123073.

58. Garrod S, Fay N, Lee J, Oberlander J, MacLeod T: **Foundations of representation: where might graphical symbol systems come from?** *Cogn Sci* 2007, **31**:961-987.

59. Fay N, Garrod S, Roberts LJ: **The fitness and functionality of culturally evolved communication systems**. *Philos Trans R Soc Lond B* 2008, **363**:3553-3561.

60. Fay N, Garrod S, Roberts LL, Swoboda N: **The interactive evolution of human communication systems**. *Cogn Sci* 2010, **34**:351-386.

61. Garrod S, Fay N, Rogers SL, Walker BP, Swoboda N: **Can iterated learning explain the emergence of graphical symbols?** *Interact Stud* 2010, **11**:33-50.

62. Theisen C, Oberlander J, Kirby S: **Systematicity and arbitrariness in novel communication systems**. *Interact Stud* 2010, **11**:14-32.

63. Caldwell C, Smith K: **Cultural evolution and perpetuation of arbitrary communicative conventions in experimental microsocieties**. *PLoS ONE* 2012, **7**:e43807.

64. Fay N, Ellison TM: **The cultural evolution of human communication systems in different sized populations: usability trumps learnability**. *PLoS ONE* 2013, **8**:e71781 http://dx.doi.org/10.1371/journal.pone.0071781.

65. Whiten A, Mesoudi A: **Establishing an experimental science of culture: animal social diffusion experiments**. *Philos Trans R Soc Lond B* 2008, **363**:3477-3488.

66. Horner V, Whiten A, Flynn EG, de Waal FBM: **Faithful replication • of foraging techniques along cultural transmission chains by chimpanzees and children**. *Proc Natl Acad Sci U S A* 2006, **103**:13878-13883.

Horner *et al*. constructed two independent transmission chains of captive chimps, where the each chimp demonstrates a behaviour for the next chimp in a chain, and seeded those chains with two different techniques for opening an ‘artificial fruit’ puzzle box; they found that those techniques were faithfully transmitted across 5–6 simulated generations, indicating a capacity for social learning sufficient to maintain stable behavioural traditions.