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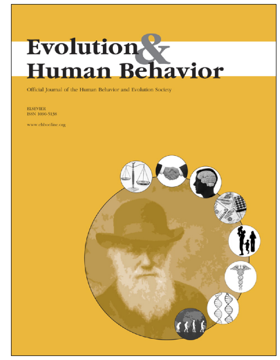

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APPLYING THE CULTURAL RATCHET TO A SOCIAL ARTEFACT: THE CUMULATIVE CULTURAL EVOLUTION OF A LANGUAGE GAME

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ABSTRACT

Material artefacts evolve by cumulative cultural evolution (CCE), the accumulation of adaptive modifications over time. We present a large-scale experiment investigating the CCE of a social artefact in transmission chains, each containing 8 adult human participants (N=408). The social artefact is what Wittgenstein calls a 'language game', the subset of language used to perform a particular activity; in the present study the language game is to communicate a route on a map. Two social learning conditions were compared: Observational Learning and Social Coordinative Learning. Participants tried to accurately communicate a route on a map to the next person in their transmission chain. Over the experimental generations the routes were reproduced with progressively higher accuracy in both conditions, demonstrating the CCE of the language game. The rate of CCE was comparable across conditions, but route reproduction accuracy was consistently higher in the Social Coordination condition compared to the Observation condition. In both conditions performance improved due to the accumulation of adaptive patterns of verbal route descriptions, and the progressive elimination of non-adaptive patterns. Whereas change in the content of the language game was similar across conditions, change to the communication process differed between the Observation and Social Coordination conditions. In conclusion, like material artefacts, social artefacts, in our case the language game, evolve by cumulative cultural evolution.

Over time artefacts in material culture have become better adapted for purpose. This is seen in the progressive improvement of the hammer, evolving from a unshaped pounding stone to a stone-and-stick composite to modern metal and mechanical forms (Basalla, 1988). This historical process is known as cumulative cultural evolution (CCE): the accumulation of adaptive modifications over time (Tennie, Call, & Tomasello, 2009; Tomasello, 1999). Cumulative cultural evolution has also been demonstrated under controlled laboratory conditions (Caldwell & Millen, 2008; Morgan et al., 2015; Muthukrishna, Shulman, Vasilescu, & Henrich, 2014). These studies focus on the cultural evolution of material artefacts. This paper adopts a similar experimental methodology to study the CCE of a social artefact. More specifically, we demonstrate the CCE of a 'language game' (Wittgenstein, 1953): the use of an increasingly effective subset of linguistic expressions and procedures for accurately communicating routes on a map.

First, we review the literature on the CCE of material and social artefacts. Next, we consider the social learning strategies likely to underpin CCE, and the laboratory experiments designed to evaluate their influence. We then explain the present study, report its findings, and discuss their significance.

Cumulative Cultural Evolution of Material and Social Artefacts

Cumulative cultural evolution (CCE) occurs when the achievements of prior generations are improved by subsequent generations to create artefacts that no single individual could invent on their own. While great apes have cultural traditions, these have remained simple, and lack the progressive adaptation that is pervasive across the human lineage (Whiten, 2005; Whiten et al., 1999), suggesting that CCE may rely on social learning mechanisms that are uniquely human (Boyd & Richerson, 1996; Tomasello, 1999). Cumulative cultural evolution – like other forms of evolution – combines innovation with faithful transmission (Tennie et al., 2009; Tomasello, 1999). The high fidelity transmission of cultural artefacts (material or social) is essential to ensure that improvements survive long enough to acquire further adaptive modifications, or 'ratchet up' (Lewis & Laland, 2012).

The literature on CCE has tended to focus on the functional adaptation of material artefacts, such as clothing (Gilligan, 2010), stone tools (Stout, Toth, Schick, & Chaminade, 2008) and kayaks (Richerson & Boyd, 2005). This process has been simulated under laboratory conditions (Caldwell & Millen, 2008; Morgan et al., 2015; Muthukrishna et al., 2014). Simulating intergenerational transmission in the laboratory lets researchers manipulate different factors hypothesized to be causal in cultural transmission and thus to investigate its mechanisms (for reviews see Mesoudi & Whiten, 2008; Whiten & Mesoudi, 2008). In one study human participants tried to build a paper plane that flew as far as possible, or a spaghetti tower that was as tall as possible (Caldwell & Millen, 2008). Participants were arranged into transmission chains, where each participant had the opportunity to learn by observing the previous participant's artefact (paper plane or spaghetti tower). CCE was observed: across the experimental generations, the paper planes flew further, and the spaghetti towers became taller. The progressive improvement in the performance of the material artefacts was driven by faithful cultural transmission combined with adaptive modification across the experimental generations.

Less is known about the CCE of social artefacts, such as cultural practices or customs. It is not clear, for example, if religious practices or monetary systems have evolved by CCE. Despite the importance of precise communication to the functional adaptation of material artefacts (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Goren-Inbar, 2011; Morgan et al., 2015), the functional evolution of language for communication is controversial in linguistics (Berwick, Friederici, Chomsky, & Bolhuis, 2013; Christiansen & Chater, 2008; Pinker & Jackendoff, 2005). Uncertainty over the CCE of language may be due to the sheer size and complexity of modern language systems. If we are to understand how language evolved and has changed over time, it is necessary to understand the role that CCE has played, and overcome the problem posed by the complexity of natural languages. Rather than looking at the language system as a whole, we focus instead on the subset of language used within the context of a specific activity; what Wittgenstein calls a 'language game' (Wittgenstein, 1953; see also Levinson, 1979).

In the present study, participants engaged in a language game that involved describing a route on a map to another person, such that the route could be accurately reproduced. As we shall see, there is considerable variation in the accuracy of the route reproductions, explainable in terms of differences in the content and process used to communicate the routes. Although human communication systems become more efficient through use (Garrod, Fay, Lee, Oberlander, & MacLeod, 2007; Piantadosi, Tily,

& Gibson, 2011; Zipf, 1949), it is not clear if they evolve by CCE (although experimental-semiotic studies with artificial languages provide some support; Fay & Ellison, 2013; Fay, Garrod, & Roberts, 2008; Fay, Garrod, Roberts, & Swoboda, 2010; Kirby, Cornish, & Smith, 2008; Tamariz, Ellison, Barr, & Fay, 2014). In the experiment reported, if the language game evolves by CCE this will be reflected by a progressive improvement in the accuracy with which the routes are reproduced across the experimental generations.

Social Learning Mechanisms for Cumulative Cultural Evolution

Two broad types of social learning are considered: observational learning and social coordinative learning. Observational learning, by emulation or by imitation (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009), concerns the traits that are acquired by observing the behaviour of a model without interaction (Bandura, 1977). This is an individual-level social learning strategy. By contrast, social coordinative learning is learning that arises when agents interact to coordinate, or align, their perspectives. Compared to observational learning, social coordinative learning is a more sophisticated inter-individual social learning strategy (Tomasello, Kruger, & Ratner, 1993).

Whereas studies have suggested that observational learning is sufficient for the cumulative cultural evolution (CCE) of simpler material artefacts (Caldwell & Millen, 2009), social coordinative learning may be crucial to the CCE of more complex material artefacts. In a recent study, participants tried to manufacture a stone tool technology using Oldowan stone knapping skills across a range of social learning conditions (Morgan et al., 2015). The social transmission of tool-making skills was enhanced by bidirectional social interaction. There was no evidence that observation alone improved social transmission, highlighting the potential importance of social coordinative learning to the CCE of complex material artefacts.

In referential communication games, social interaction trumps observation: communication success is higher among active conversationalists compared to passive observers of the same conversation (Garrod et al., 2007; Schober & Clark, 1989). It is argued that active participation during information exchange allows shared meanings to be mutually agreed, or grounded (Clark, 1996). A similar pattern is observed in a multi-generational communication game (Tan & Fay, 2011). Here, a narrative text was reproduced with higher fidelity across 4-generation transmission chains when participants could directly interact with the adjacent chain member compared to when they could not. These studies indicate that social interaction improves transmission fidelity, a crucial component of CCE (Lewis & Laland, 2012).

In the present study, social interaction allowed participants to negotiate a route description language game with their partner. For example, a participant might indicate uncertainty about a route description at a particular point by asking a question or requesting a clarification. Their partner can then revise their route description, or generate an alternative description, and this process can be repeated until the route description is mutually agreed. Interactive negotiation like this offers a mechanism through which modifications and innovations arise and are selected. This negotiation process may also act as a mechanism to eliminate less-adaptive route descriptions, with route descriptions that are not mutually agreed being discarded. Crucially, this social coordinative selection process is not available to passive observers: they must rely solely on individual inference.

The Current Study

We present a large-scale experimental study that tests for the cumulative cultural evolution (CCE) of a language game (N=408). Participants were organized into 8-person (or generation) transmission chains. Their task was to accurately communicate a route on a map to the next participant in the chain (referred to as the Instruction-Giver and Instruction-Follower), who tried to reproduce the route on their map. Once Instruction-Followers were done, they would become Instruction-Givers, and communicate a different route to the next participant in the chain. Each Instruction-Giver in a chain saw a distinct route on a different map. Increased accuracy of route reproductions across the experimental generations would indicate cumulative refinements of the linguistic procedures used and transmitted. We predict that the language game will evolve by CCE. If correct, there will be an improvement in route reproduction accuracy across the experimental generations (Hypothesis 1).

The transmission chains were divided into two conditions. In the *Social Coordination* condition, the Instruction-Follower could directly interact with the Instruction-Giver. In the *Observation* condition, Instruction-Followers could observe the route descriptions from the Instruction-Giver, but they could not respond to or question the Instruction-Giver. We predict that task performance will be modulated by condition (Hypothesis 2). If route reproduction accuracy is higher in the Social Coordination condition compared to the Observation condition, we can conclude that social coordination improves social learning. If route reproduction accuracy improves more rapidly in the Social Coordination condition, we can conclude that social coordination accelerates the CCE of the language game.

We then consider the factors that give rise to the progressive improvement in route reproduction accuracy across the experimental generations and between the experimental conditions. It has been shown that the use of some lexical terms positively affects performance on a joint task, while other terms negatively affect performance (Fusaroli et al., 2012). The extent to which individual lexical terms are associated positively or negatively with task performance can be measured computationally. We can then test the hypothesis that terms that positively contribute to route reproduction accuracy will accumulate, while terms that negatively affect route reproduction accuracy will be eliminated across the experimental generations (Hypothesis 3). A benefit of social coordinative learning over observational learning is that the Instruction-Giver and -Follower can negotiate route description terms, and this may act as a selection mechanism (in addition to Instruction-Follower inference). If correct, more positive route description terms and fewer negative terms will be evident in the Social Coordination condition compared to the Observation condition (Hypothesis 4).

Like vocabulary, message structure can affect communicative success. Conversation is the basic medium of human communication (Clark, 1996; Pickering & Garrod, 2004), so we were interested in how Instruction-Givers in the Observation condition might adapt the route description process to the non-interactive context. A series of exploratory analyses are reported that test for changes to the communication process across the experimental generations and between the experimental conditions.

METHOD

The study received approval from the University of Western Australia Ethics Committee. Participants viewed an information sheet before giving written consent to take part in the study. The information sheet and consent form were both approved by the Ethics Committee. All methods were performed in accordance with the guidelines from the NHMRC/ARC/University Australia's National Statement on Ethical Conduct in Human Research.

PARTICIPANTS

A convenience sample of four hundred and eight undergraduate psychology students (287 females) participated in exchange for partial course credit. Participants ranged in age from 18 to 57 years (*M*= 21.56, *SD*= 4.41).

TASK

Participants were tasked with accurately communicating a route on a map to their partner. The Instruction-Giver's map contained a route and between 11 and 13 landmarks (simple line drawings of lakes, cottages, telephone boxes, etc.). The Instruction-Follower's map contained only the landmarks, and no route. All routes had specific start and end points marked clearly on both the Instruction-Giver and Instruction-Follower's maps. In prior studies using the Map Task the landmarks were labeled with their name, and the set of landmarks differed in the maps of the Instruction-Giver and Instruction-Follower (Anderson, Bader, et al., 1991; Louwerse, Dale, Bard, & Jeuniaux, 2012). In our study, the landmarks were not named, and both participants' maps contained the same set of landmarks. Landmark labels were removed to increase task difficulty, and having participants share the same set of landmarks was done to ensure the task did not advantage participants in the Social Coordination condition over those in the Observation condition. Participants were told that their task was to accurately reproduce the Instruction-Giver's route on the Instruction-Follower's map.

PROCEDURE

Fifty-one eight-person transmission chains were tested. Participants were randomly assigned to a condition (Social Coordination, Observation; 25 and 26 transmission chains respectively) and to a position in the chain (1-8).

In each condition the task was done pair-by-pair. Each participant was seated at a different computer terminal and all communication took place using an Internet textbased chat program (http://xchat.org/). Route description information appeared on the Instruction-Follower's screen after the Instruction-Giver pressed the return key (at which point the typed instructions were sent to the Instruction-Follower). In the Social Coordination condition the Instruction-Follower could interact with the Instruction-Giver: using the same text-chat tool they could ask questions, seek clarification of route descriptions etc. In the Observation condition the Instruction-Follower was not permitted to use the text-chat tool; they were restricted to passively processing the Instruction-Giver's instructions as they appeared on their screen (i.e., each time the Instruction-Giver sent a 'packet' of information). Thus, participants in the Observation condition could not affect the route descriptions they received. The participant's map was presented alongside the text-chat tool (to the right of the text-chat interface). The maps were presented as consistently-sized .gif images using the Microsoft Paint program. Using the computer mouse, the Instruction-Follower drew the route described by the Instruction-Giver onto their map. Instruction-Followers were told not to delete any part of the drawn route; if they thought they had made a mistake they were told to continue from that point.

Each pair of participants was given 10 minutes to complete the task, after which their communications and the reproduced routes were saved. The Instruction-Giver then left the experiment, and the Instruction-Follower became the Instruction-Giver to a new Instruction-Follower. The new Instruction-Giver then communicated a route from a new and different map to the new Instruction-Follower. This process was repeated for the 7 pairs constituting the 8-generation transmission chain. To promote the evolution of a general route description language game, eight different maps were used, and the maps were randomly sampled (without replacement) and randomly assigned to a position in each transmission chain (see SM1).

Quantifying Route Reproduction Accuracy

Route reproduction accuracy was quantified as a function of how far the Instruction-Follower's reproduced route deviated from the Instruction-Giver's route (Anderson, Clark, & Mullin, 1991). The deviation score in the present study is the number of pixels between the two routes. Our performance measure (expressed as a fraction of pixels) was one minus the deviation score divided by the total pixel count (the same for all maps). A higher performance measure reflects a more accurate route reproduction (see **Figure 1**).

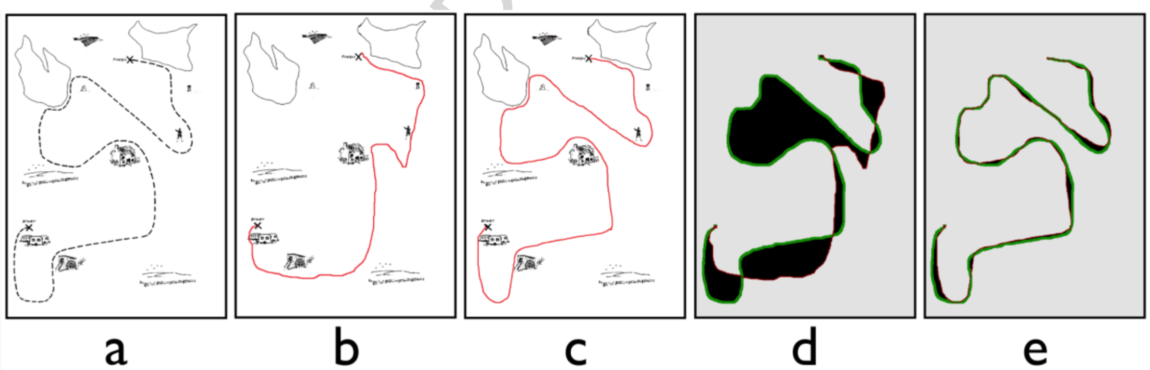

Figure 1. Example Instruction-Giver Map (Panel a) and the reproduced route by an Instruction-Follower at Generation 1-2 (Panel b) and at Generation 7-8 (Panel c) across two separate transmission chains (from the Observation condition). The Instruction-Follower's reproduced route (in red) was superimposed onto the Instruction-Giver's route (transformed to a solid green line). The deviation score (in pixels) was calculated

(black area) and subtracted from the total number of pixels to give a route reproduction accuracy score (grey area; see Panel d and e). A lower deviation score returned a higher accuracy score (expressed as a fraction of total pixels). In this example, route reproduction accuracy was higher at Generation 7-8 (Panel e) than at Generation 1-2 (Panel d). The stimuli in Figure 1, and in Supplementary Materials 1, were downloaded from the HCRC website (http://groups.inf.ed.ac.uk/maptask/index.html). They were modified for our study and are reproduced here under a creative commons license (https://creativecommons.org/licenses/by-nc-sa/2.5/).

Identifying Lexical Terms That Positively or Negatively Affected Route Reproduction Accuracy

Instruction-Givers used a variety of descriptive word types to communicate the route to the Instruction-Follower: distance (e.g., cm, close), direction (e.g., left/right, towards), shape (e.g., curve, slant), position (e.g., outer, alongside), preposition (e.g., onto, underneath), landmark (e.g., bridge, pond) and interactive feedback (e.g., ok?, done). Some lexical terms may have positively contributed to task performance whereas others may have negatively affected performance. If the language game evolves by cumulative cultural evolution (CCE), then lexical terms that positively contributed to route reproduction accuracy will accumulate, and terms that negatively affected route reproduction accuracy will be eliminated. The extent to which an individual lexical term was associated positively or negatively with route reproduction accuracy was measured computationally (see SM2 for details).

RESULTS

The data was analyzed using linear mixed effects modeling. All analyses were conducted in R (R Core Team, 2013) and models were estimated using the lmer() function of lme4 (Bates, Maechler, Bolker, & Walker, 2013). P-values were obtained by likelihood ratio tests of the full model against the model without the predictor(s). All predictors were centered prior to analysis. A maximal random effects structure was specified where possible (Barr, Levy, Scheepers, & Tily, 2013). The variance accounted for by the best-fitting model was calculated using the r.squaredGLMM() function in MuMIn (Bartoń, 2013).

Section 1 tests for the progressive improvement in route reproduction accuracy across the experimental generations, and route accuracy differences between the Social Coordination condition and Observation condition. Sections 2 and 3 examine the functional adaptation of the language game that gives rise to the progressive improvement in route reproduction accuracy.

Section 1. Progressive Improvement in Route Reproduction Accuracy

The route reproduction accuracy scores exhibited strong negative skew (-2.260). This was normalized by Logit transformation (-0.058), making the data suitable for parametric statistical tests (Tabachnick, Fidell, & Osterlind, 2001). Condition (Social Coordination, Observation), Generation (1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8) and their interaction were entered as fixed effects. The best fitting model specified Condition and

Generation as fixed effects without interaction, accounting for 28.29% of the variance in the route reproduction accuracy scores (see SM3 for the full model specification and model output). Removing the fixed effect of Condition or the fixed effect of Generation reduced model fit, $\chi^2(1)= 8.978$, $p= .003$ and $\chi^2(1)= 24.377$, $p< .001$. The same pattern of results was returned by the raw, untransformed route reproduction accuracy scores (see SM4). The routes were reproduced with higher accuracy across the experimental generations in both conditions, supporting Hypothesis 1. Overall route reproduction accuracy was higher in the Social Coordination condition compared to the Observation condition, supporting Hypothesis 2, but social coordinative learning did not accelerate CCE (see **Figure 2**).

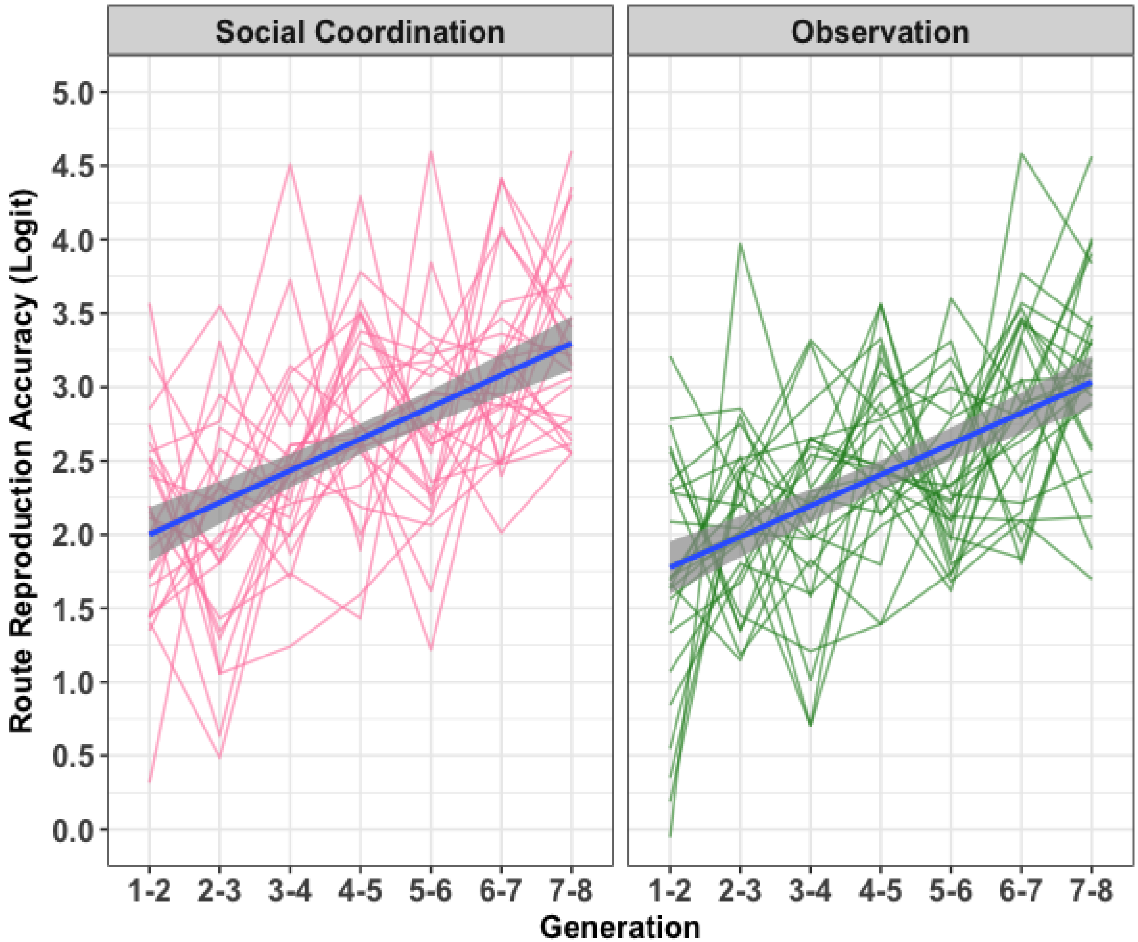

Figure 2. Change in route reproduction accuracy (expressed as Logit scores and plotted for each transmission chain) across the experimental generations in the Social Coordination and Observation conditions. The blue straight line is the linear model fit and the light grey shaded area is the 95% confidence interval.

Cultural Inheritance of Route Reproduction Accuracy. For the language game to survive long enough to acquire further adaptive modifications, it must be transmitted between the experimental generations with some level of fidelity. If route reproduction accuracy at Generation N-plus-1 is predicted by route reproduction accuracy at Generation N, this would be evidence supporting the cultural inheritance of the language game.

The route reproduction accuracy scores at Generation N-plus-1 were our dependent variable. Condition (Social Coordination, Observation) and the route reproduction accuracy scores at Generation N were entered as fixed effects with interaction. The best fitting model specified Condition and Generation N Performance (route reproduction accuracy) as fixed effects without interaction, accounting for 6.05% of the variance in route reproduction accuracy scores at Generation N-plus-1 (see SM5). Removing the fixed effect of Condition or the fixed effect of Generation N Performance reduced the model fit, $\chi^2(1)= 5.347$, $p= .021$ and $\chi^2(1)= 13.945$, $p< .001$. As before, route reproduction accuracy was higher in the Social Coordination condition compared to the Observation condition, and route reproduction accuracy was predicted by the route reproduction accuracy of the prior generation, demonstrating cultural inheritance.

The Cumulative Cultural Evolution of the Language Game

Two mechanisms that might explain the progressive improvement in route reproduction accuracy are considered: the content communicated by Instruction-Givers (Section 2) and the process used to communicate the route information (Section 3).

Section 2: Adaptive Change in the Content Communicated by Instruction-Givers

Because the total number of words used to communicate the different routes was higher for Instruction-Givers in the Social Coordination condition compared to the

Observation condition ($M_{\text{Social Coordination}}$= 251.49 words, *SD*= 96.61 and $M_{\text{Observation}}$= 200.23 words, *SD*= 69.16; see SM6 for data visualization and statistical analysis), we computed the density of positively- and negatively-biased tokens (positively- and negatively-biased words, including repetitions, as a percentage of total Instruction-Giver words) for each Instruction-Giver at each generation. We then compared the change in the density of positively- and negatively-biased route description tokens over generations in the different conditions.

The density of Positively- and Negatively-biased route description tokens was our dependent variable. Condition (Social Coordination, Observation), Token Polarity (Positive, Negative) and Generation (1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8) with interaction were entered as fixed effects. The best fitting model specified Token Polarity and Generation as fixed effects with interaction plus Condition and Token Polarity as fixed effects with interaction, accounting for 69.57% of the variance in token density (see SM7 for the full model specification and model output). Removing the interaction between either pair of fixed effects reduced model fit, $\chi^2(1)$= 25.13, p< .001 and $\chi^2(1)$= 4.73, p= .029. The Token Polarity by Generation interaction is explained by the increase in the density of positively-biased route description tokens, and the decrease in the density of negatively-biased route description tokens over generations in both conditions, supporting Hypothesis 3. The Condition by Polarity interaction is explained by the higher density of positively-biased tokens and the lower density of negatively-biased tokens in the Social Coordination condition compared to the Observation condition, supporting Hypothesis 4 (see **Figure 3**) (see SM8).

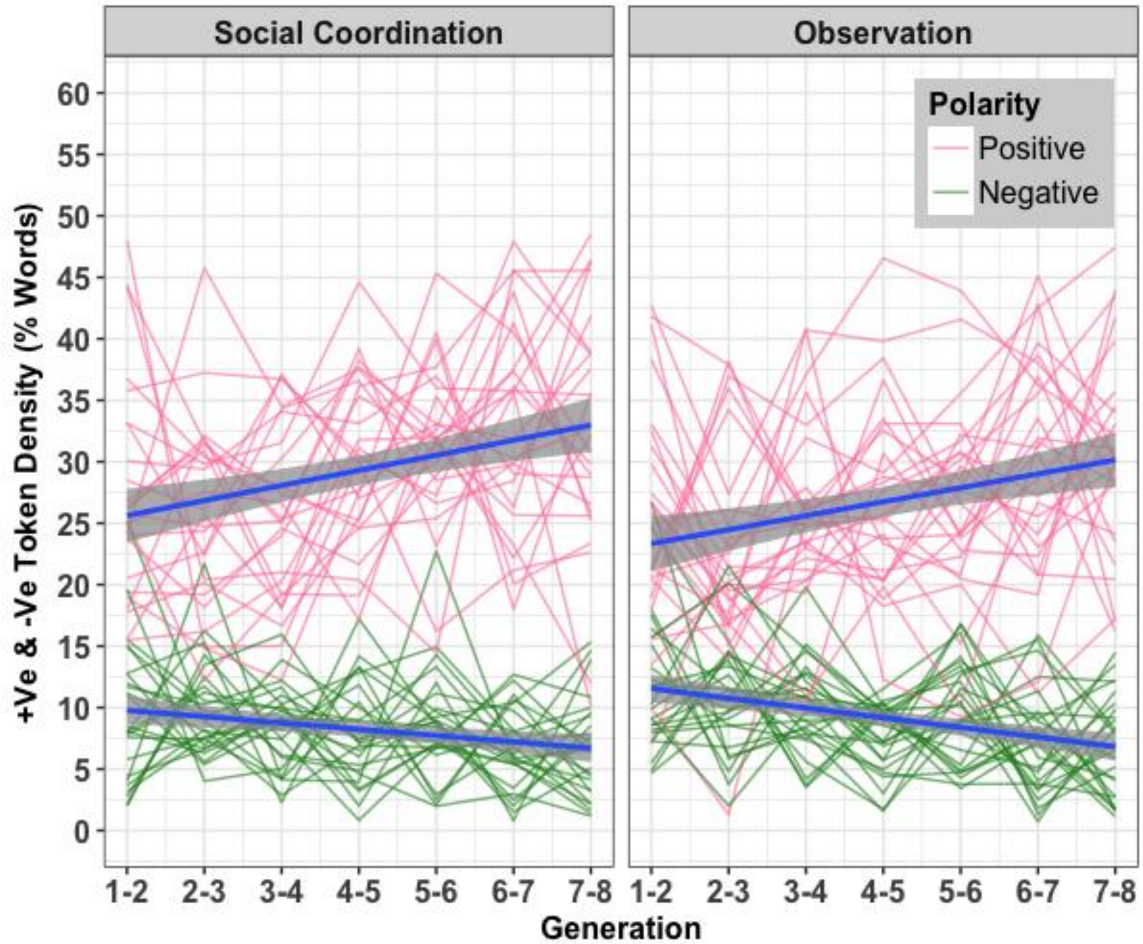

Figure 3. Change in the density of Positively- and Negatively-biased route description word tokens (as a % of total words tokens and plotted for each transmission chain) produced by Instruction-Givers across generations in the Social Coordination and Observation conditions. The blue straight line is the linear model fit and the light grey shaded area is the 95% confidence interval.

Cultural Inheritance of Positively- and Negatively-Biased Route Description Tokens. If the distributions of positively-biased route description tokens are inherited by the next generation and the distributions of negatively-biased route description tokens are not, this would suggest the language game evolved by cultural selection.

Token density at Generation N-plus-1 was our dependent variable. Generation N Token Density, Condition and Token Polarity were entered as fixed effects with interaction. The best fitting model specified Generation N Token Density and Token Polarity with interaction, accounting for 70.83% of the variance in token density at Generation N-plus-1 (see SM9 for the full model specification and model output). Removing the Generation N Token Density by Token Polarity interaction reduced model fit, $\chi^2(1)= 7.015$, $p= .008$. Further analysis indicated that positively-biased token density at Generation N-plus-1 was predicted by positively-biased token density at Generation N. By contrast, negatively-biased token density at Generation N-plus-1 was not predicted by negatively-biased token density at Generation N (see SM10).

In both conditions, positively-biased route description tokens were inherited from the prior experimental generation, but negatively-biased route description tokens were not. This pattern of results suggests that cultural selection was filtering components of the language game.

Profile of Positively- and Negatively-Biased Route Description Terms. What constitutes a positively-biased or negatively-biased route description, and do they differ between the Social Coordination and Observation conditions? **Figure 4** illustrates the change in positively- and negatively-biased route description lexical terms over generations in the different conditions, using the route description types described earlier (e.g., direction, distance, shape). Also included is an ‘other’ category to capture lexical terms that fell outside of these categories. Author NF and author TME independently coded the different route description terms into one of eight categories. Substantial inter-coder agreement was observed (K= .663, k= 2, N= 551) (Viera & Garrett, 2005). The conditions exhibited a similar profile of positively- and negatively-biased route description terms, but with a higher density of positively-biased terms in the Social Coordination condition and a lower density of negatively-biased terms in this condition (compared to the Observation condition). This suggests that the difference between the conditions is quantitative rather than qualitative.

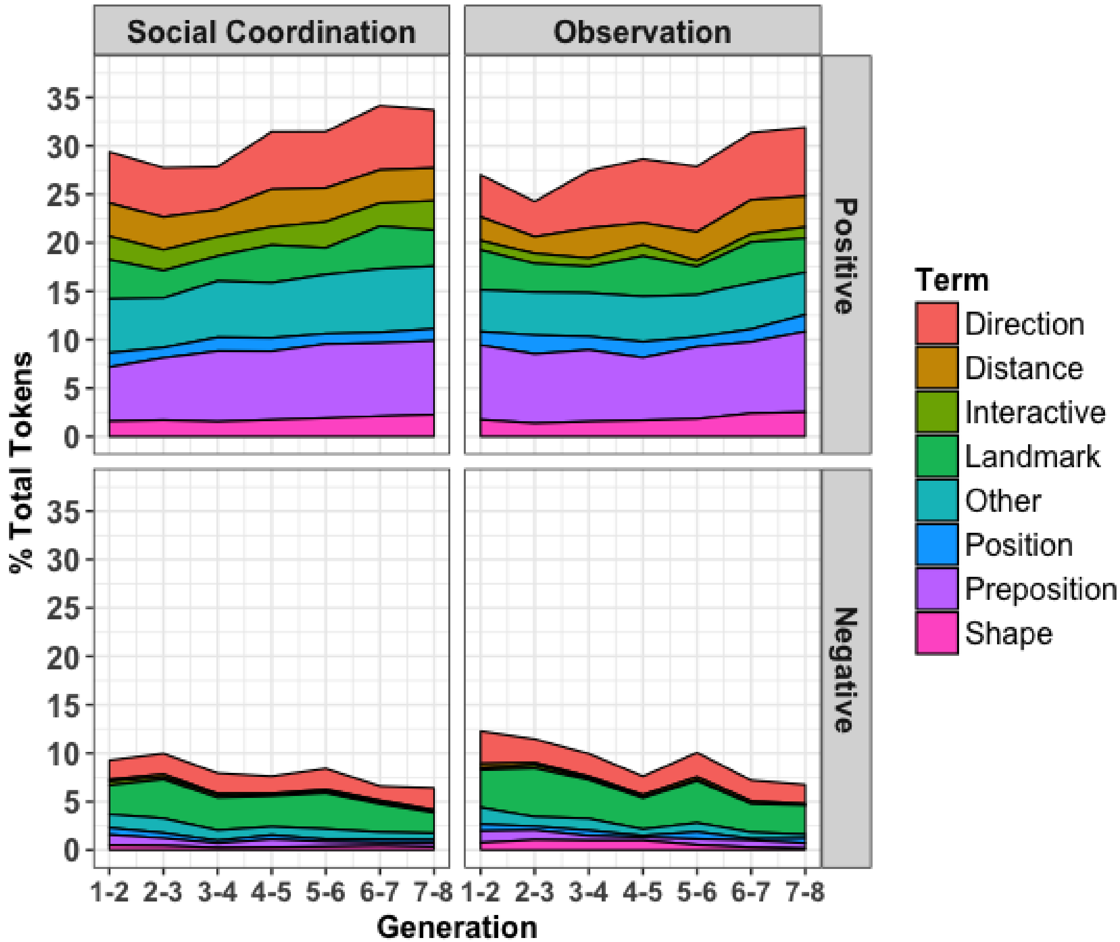

Figure 4. Change in the mean density of Positively- and Negatively-biased route description terms (as a % of total tokens) for each category of description type, produced by Instruction-Givers across generations in the Social Coordination and Observation conditions.

Section 3: Adaptive Change to the Communication Process

A series of exploratory analyses test for changes to the communication process across the experimental generations and between the experimental conditions. First, we examined the adaptive influence of social interaction on route reproduction accuracy, and whether social interaction became a cultural tradition in the Social Coordination condition. Next we examined how Instruction-Givers packaged their route descriptions for the Instruction-Follower, and whether this changed over generations. We then examined the adaptive influence of packet size (mean number of words per information transmission episode by Instruction-Givers) on route reproduction accuracy, and the extent to which packet size became a cultural tradition.

Social Interaction. Communication between Instruction-Givers and Instruction-Followers in the Social Coordination condition was tightly coupled; the mean number of information packets sent was 20.80 for Instruction-Givers and 12.18 for Instruction-Followers, and these were strongly correlated, $r(173)= .65$, $p< .001$.

Was more frequent social interaction associated with higher route reproduction accuracy? To answer this, we operationalized the frequency of social interaction as the ratio of Instruction-Giver to Instruction-Follower packets sent, and entered this as a fixed effect in a mixed effects model where route reproduction accuracy was the dependent variable. Compared against a null model, including the frequency of social interaction improved model fit, $\chi^2(1)= 6.942$, $p= .008$, accounting for 3.21% of the variance in the route reproduction accuracy scores (see SM11 for the full model specification and model output). Despite the benefit of social interaction to route reproduction accuracy, there was no evidence of a statistical change in Instruction-Giver and Instruction-Follower interactivity over generations (ratio of Instruction-Giver to Instruction-Follower packets sent: $M_{Generation1\text{-}2}= 0.59$, $SD= 0.32$ and $M_{Generation7\text{-}8}= 0.58$, *SD*= 0.27; see SM12 for data visualization and statistical analysis). The finding that interactivity did not evolve cumulatively suggests that it is not amenable to social learning.

Route Information Packaging. Communication in the Social Coordination condition was characterized by short Instruction-Giver route descriptions (M= 20.80 packets, with M= 13.71 words per packet) accompanied by shorter Instruction-Follower feedback (M= 12.18 packets, with M= 4.06 words per packet). This conversation style was consistent across transmission chains and generations in the Social Coordination condition (see **Figure 5**). By contrast, Instruction-Givers in the Observation condition did not receive Instruction-Follower feedback. In this condition there was a systematic change in the process used to transmit the route descriptions, from a conversation style to a narrative style. Initially short route descriptions were given by Instruction-Givers ($M_{Generation1\text{-}2}$= 13.81 packets, with M= 13.35 words per packet), but over the experimental generations the number of route description packets decreased and the size of each packet increased ($M_{Generation7\text{-}8}$= 5.00 packets, with M= 49.49 words per packet). This change in the route description process was consistent across Instruction-Givers in the Observation condition (see **Figure 5**).

Mean Instruction-Giver packet size (in words) was our dependent variable. Condition (Social Coordination, Observation) and Generation (1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8) with interaction were entered as fixed effects. The best fitting model specified Condition and Generation as fixed effects with interaction, accounting for 51.88% of the variance in Instruction-Giver packet size (see SM13 for the model specification and model output). Removing the interaction between Condition and Generation reduced the model fit, $\chi^2(1)= 49.36$, $p< .001$. To understand the interaction effect we analyzed each condition separately. In the Social Coordination condition the full model did not differ from the null model, $\chi^2(1)= 0.25$, $p= .618$, indicating no evidence for a statistical change in Instruction-Giver packet size over generations. By contrast, the Observation condition differed from the null model, $\chi^2(1)= 27.87$, $p< .001$; in this condition the mean Instruction-Giver packet size significantly increased over generations. **Figure 5** suggests the increase in Instruction-Giver packet size is non-linear, with the slope of the regression line becoming steeper from Generation 5-6. Growth curve analysis indicated that adding a quadratic term for generation to the model improved model fit over a simple linear model, $\chi^2(1)= 43.68$, $p< .001$ (see SM14 for the model specification and model output) (Winter & Wieling, 2016).

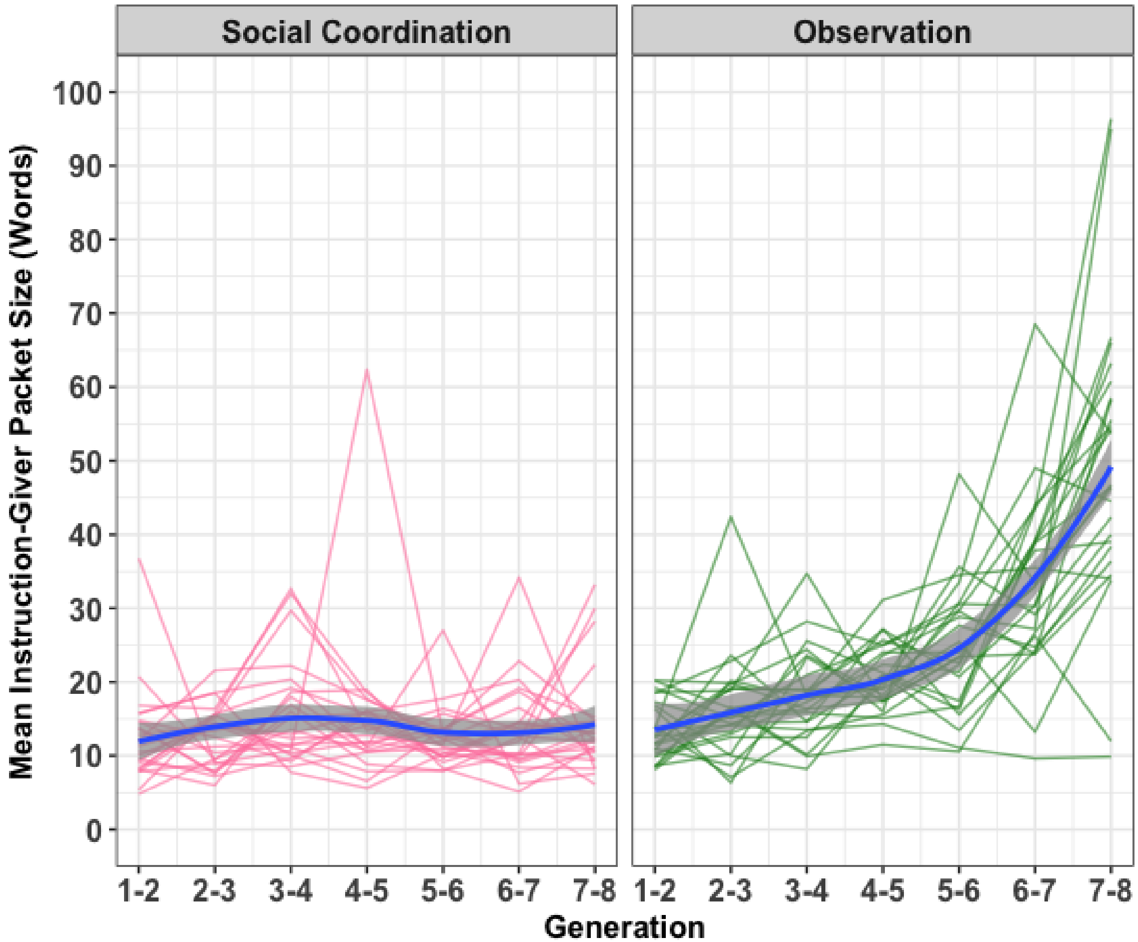

Figure 5. Change in Instruction-Giver mean packet size (in words) across generations in the Social Coordination and Observation conditions (plotted for each transmission chain). The blue line is the smoothed model fit and the light grey shaded area is the 95% confidence interval.

Cultural Inheritance of Instruction-Giver Packet Size in the Observation Condition. If Instruction-Giver packet size at Generation N-plus-1 is predicted by Instruction-Giver packet size at Generation N, this would be evidence of the cultural inheritance of the language game.

Instruction-Giver packet size at Generation N-plus-1 was our dependent variable, and Instruction-Giver packet size at Generation N was entered as a fixed effect (see SM15 for the full model specification and model output). Compared against a null model, including Packet Size at Generation N improved model fit, $\chi^2(1)= 78.838$, $p< .001$, accounting for 39.92% of the variance in Instruction-Giver packet size at Generation N-plus-1, demonstrating robust cultural inheritance.

Instruction-Giver Packet Size and Route Reproduction Accuracy. Does the increase in Instruction-Giver packet size over generations in the Observation condition reflect a functional adaptation to the non-interactive context? To test this, we entered Packet Size as a fixed effect in a linear mixed effects model where route reproduction accuracy was the dependent variable (see SM16 for the full model specification and model output). Compared against a null model, including Packet Size improved model fit, $\chi^2(1)= 51.245$, $p< .001$, accounting for 21.13% of the variance in the route reproduction accuracy scores. To examine the causal influence of packet size on route reproduction accuracy we tested if Packet Size at Generation N predicted route reproduction accuracy at Generation N-plus-1 (where Instruction-Giver packet size preceded task performance; see SM17 for the full model specification and model output). Compared against a null model, including Packet Size at Generation N improved model fit, $\chi^2(1)= 26.386$, $p< .001$, accounting for 13.34% of the variance in the route reproduction accuracy scores at Generation N-plus-1. The increase in Instruction-Giver packet size over generations in the Observation condition reflects a functional adaptation to the non-interactive context.

Finally, we tested if packet size positively contributed to route reproduction accuracy over and above the content communicated by Instruction-Givers in the Observation condition. First, the influence of the density of positively- and negatively-biased route description tokens (as a percentage of total tokens) on the route reproduction accuracy scores in the Observation condition was modeled to provide a baseline. Positive and Negative route description token density were entered as fixed effects with interaction. The best fitting model specified Positive and Negative token density as fixed effects with interaction, accounting for 38.14% of the variance in the route accuracy scores (see SM18 for the model specification and model output). Removing the interaction between Positive and Negative token density reduced the model fit, $\chi^2(1)= 4.89$, $p= .027$. Next, Packet Size (at Generation N) was added to the model as a fixed effect. This improved the model fit over the baseline model, $\chi^2(1)= 31.39$, $p< .001$, accounting for 47.05% of the variance in the route reproduction accuracy scores (at Generation N) (i.e., explaining an additional 8.91% of the variance in route reproduction accuracy). The increase in packet size positively contributed to route reproduction accuracy, and did so over and above the content communicated by Instruction-Givers in the Observation condition.

DISCUSSION

We set out to investigate the cumulative cultural evolution (CCE) of a cultural artefact – the subset of language used to communicate routes on a map – and its mechanisms. Instruction-Giver routes were reproduced with progressively higher accuracy by Instruction-Followers across the experimental generations in both conditions, demonstrating the CCE of the language game. Although social coordinative learning did not accelerate the CCE of the language game, route reproduction accuracy was consistently higher in this condition compared to the Observation condition. This demonstrates a clear benefit of social coordinative processes to social learning. Cultural inheritance of route reproduction accuracy was observed (both conditions). In addition, cultural selection acted to filter adaptive components of the language game (both conditions). Whereas changes to the language game content were similar over generations in both conditions, changes to the communication process differed between the Social Coordination and Observation conditions.

The Cumulative Cultural Evolution of the Language Game

Social interaction allowed the Instruction-Giver and Follower to negotiate route description terms, and this acted as a cultural selection mechanism. This opportunity was not available to participants in the Observation condition, who relied exclusively on individual inference. That is, whereas adaptation and elimination of lexical terms could happen instantaneously through interactive negotiation in the Social Coordination condition, in the Observation condition any ambiguous or non-functional description terms could only be eliminated in the subsequent trial, i.e., when the Instruction-

Follower became Instruction-Giver and could decide which lexical terms to use in their own route descriptions.

Lexical terms that positively contributed to route reproduction accuracy accumulated, and terms that negatively affected route reproduction accuracy were progressively eliminated across the experimental generations (both conditions). The cultural inheritance of lexical terms that positively contributed to route reproduction accuracy was observed. By contrast, lexical terms that negatively affected route reproduction accuracy were not inherited from the prior generation; they were progressively eliminated over the experimental generations. This pattern of results indicates that cultural selection was operating on the route description terms. As predicted, social coordinative learning conferred a valuable cultural selection mechanism: the density of lexical terms that positively contributed to route reproduction accuracy was higher, and the density of lexical terms that negatively contributed to route reproduction accuracy was lower in the Social Coordination condition compared to the Observation condition. The accumulation of adaptive modifications and innovations to the language game, and the elimination of deleterious ones, drove a cumulative improvement in route reproduction accuracy over the experimental generations.

The final set of analyses tested for adaptive changes to the language game process. Conversation is the basic medium of human communication (Clark, 1996; Pickering & Garrod, 2004), so we were interested in how Instruction-Givers in the Observation condition might adapt their communication to the non-interactive context.

They changed their communication from a conversation style, characterized by frequent and succinct information exchanges, to a narrative style, characterized by infrequent but elaborate information exchanges. This process change, consistent across the transmission chains, was a powerful cultural tradition that was amplified over the experimental generations. Furthermore, this process change was adaptive, being strongly associated with route reproduction accuracy, and its positive influence on route reproduction accuracy extended beyond the adaptive changes to the route description content. By contrast, no process change was observed in the Social Coordination condition. Here, a conversation style was maintained across the experimental generations.

Transmission Chain Design Affects the Cultural Evolutionary Process

Experimental studies of cultural transmission have tended to focus on observational learning, so have relied on non-interactive transmission chain designs (Bartlett, 1932; Bebbington, MacLeod, Ellison, & Fay, 2017; Kalish, Griffiths, & Lewandowsky, 2007; Kirby et al., 2008; Mesoudi & Whiten, 2004; Ravignani, Delgado, & Kirby, 2016; Tamariz & Kirby, 2014). A benefit of this design is that non-interactive transmission chains are easier to collect than interactive transmission chain designs. Research has shown that the transmission fidelity of information is enhanced when participants can directly interact with the adjacent chain member compared to when they cannot (Tan & Fay, 2011). This suggests that the difference between the Social Coordination and Observation transmission chain designs on cultural transmission is quantitative, rather than qualitative. In the present study, a quantitative difference between the conditions was observed; the density of route description lexical terms that positively contributed to route reproduction accuracy was higher in the Social Coordination condition, and the density of lexical terms that negatively affected route reproduction accuracy was lower in this condition compared to the Observation condition. In addition, the profile of the route description lexical terms was similar across the Social Coordination and Observation conditions.

By contrast, there was a qualitative difference between the conditions in the language game process. Whereas participants in the Social Coordination condition consistently adopted a conversation style, in the Observation condition the process evolved from a conversation style to a narrative style over the experimental generations. Furthermore, this process change represented a functional adaptation to the non-interactive context. This qualitative difference between the Social Coordination condition and the Observation condition demonstrates that the transmission chain design can influence the cultural evolutionary process. Future studies using transmission chains should be aware of this, and use this information to make an informed decision about the transmission chain design that best captures the cultural evolutionary process being simulated. Experimental simulations of language evolution that have added social interaction to traditionally observation-based transmission chain designs have shown this to dramatically alter the nature of the evolved linguistic systems, from systems that are primarily driven by ease of acquisition, to systems that balance ease of acquisition with functional adaptation for use (Kirby et al., 2008; Kirby, Tamariz, Cornish, & Smith, 2015).

CONCLUSION

We conducted a large-scale experimental study (N=408) that tested for the cumulative cultural evolution (CCE) of a social artefact, a language game (Wittgenstein, 1953) in which participants communicated a route on a map to another person. Using a transmission chain design that simulated intergenerational transmission, we demonstrated that the language game evolved by CCE: the routes were reproduced with progressively higher accuracy over the experimental generations, and this was driven by adaptive modifications and innovations to the language game that accumulated over the experimental generations. Like material artefacts, the social artefact evolved by CCE. Our findings also highlight the importance of social coordinative processes to social learning: in our experiment, route reproduction accuracy was consistently higher in the Social Coordination condition compared to the Observation condition. Analysis of the changes to the language game indicated that social interaction allowed the adjacent chain members to work together to innovate mutually acceptable and adaptive route description terms. That is, social interaction added an extra selection mechanism (to individual inference) that improved overall task performance.

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