doi:10.1111/j.1558-5646.2012.01804.x

SOCIAL LEARNERS REQUIRE PROCESS INFORMATION TO OUTPERFORM INDIVIDUAL LEARNERS

Maxime Derex,[1,2] Bernard Godelle,[1] and Michel Raymond[1,3]

[1]*University of Montpellier II, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France*

[2]*E-mail: maxime.derex@gmail.com*

[3]*CNRS, Institute of Evolutionary Sciences, CC 065, Place Eugène Bataillon, Montpellier, France*

Received June 21, 2012
Accepted August 10, 2012
Data Archived: Dryad doi:10.5061/dryad.5ck3n

Humans exhibit a rich and complex material culture with no equivalent in animals. Also, social learning, a crucial requirement for culture, is particularly developed in humans and provides a means to accumulate knowledge over time and to develop advanced technologies. However, the type of social learning required for the evolution of this complex material culture is still debated. Here, using a complex and opaque virtual task, the efficiency of individual learning and two types of social learning (product-copying and process-copying) were compared. We found that (1) individuals from process-copying groups outperformed individuals from product-copying groups or individual learners, whereas access to product information was not a sufficient condition for providing an advantage to social learners compared to individual learners; (2) social learning did not seem to affect the exploration of the fitness landscape; (3) social learning led to strong within-group convergence and also to between-group convergence, and (4) individuals used widely variable social learning strategies. The implications of these results for cumulative culture evolution are discussed.

KEY WORDS: Cultural transmission, cumulative culture, emulation, imitation, social learning.

One of the crucial components of human culture is social learning, that is, learning that is influenced by the observation of, or interaction with, another individual or an individual's product (Heyes 1994). The acquisition and use of socially acquired information is commonly assumed to be profitable to individuals because it allows them to avoid the costs, in terms of the effort and risk, of trial-and-error learning. However, modeling suggests that social learning can impede progress at the group level (Boyd and Richerson 1995; Rogers 1988; but see Rendell et al. 2010). Indeed, social learning may be considered to be a form of information parasitism (Giraldeau et al. 2002), social learners being "individuals that live at the expense of the population, exploiting the information (. . .) but contributing no new information themselves" (Laland 2004). Modeling suggests that at the group level, the cost of social learning can be avoided if individuals are able to switch between individual and social learning (Feldman et al. 1996; Kameda and Nakanishi 2002, 2003; Enquist et al. 2007), which has been empirically supported using virtual tasks (Kameda and Nakanishi 2002, 2003; McElreath et al. 2005; Efferson et al. 2008; Morgan et al. 2012). However, these experiments rely on tasks displaying only a simple fitness landscape. In a more complex virtual task with multiple parameters, there is some indication (although not significant) that more frequent episodes of social learning can reduce the exploration of a rugged fitness landscape (Mesoudi 2008). As actual cultural artifacts present a multidimensional complexity, cultural evolution experiments most likely need to consider complex fitness landscapes to determine the benefits and limits of using social information.

Also previous studies provide the complete information to social learners (nonopacity), so that a simple visual contact with an item is sufficient to be able to construct an equally efficient copy. Quantitative measures of technological complexity suggest that human material artifacts are opaque compared to those of animals (Oswalt 1976), even in relatively simple material cultures such as those of hunter gatherers (Ohmagari and Berkes 1997). Thus *product-oriented copying*, where the learner has to develop the means to achieve the outcome on his/her own, provides poorer information than *process-oriented copying,* where the learner benefits from the means to reconstruct the end product (Tennie et al. 2009). One experimental study has compared the efficiency of these two types of social learning in a task where participants had to make paper planes and found no difference between the two conditions (Caldwell and Millen 2009). However, in this task, the final product was nonopaque and provided the whole of information necessary to reconstruct a same one (location of the folds, angle, sequence of construction). The well-documented loss of technologies observed among the Polar Inuit of Northwest Greenland illustrates the crucial role of knowledge transmission in an opaque task. In 1820, an epidemic carried away the older, knowledgeable members of the group, stopping the transmission across generations of how to build essential and complex artifacts (Rasmussen et al. 1908). Young adults could not make their own artifacts, and the existing artifacts were rapidly disappearing, as they were buried with their owners according to the custom. As a consequence, for more than 40 years, the Polar Inuit lived without kayaks, leisters, and bows and arrows. They collectively remembered kayaks, leisters, and bows and arrows, but they did not know how to make them. Visual access to an object can thus provide information about the means used to create it, but such information is often only partial. In this case, information collected by scroungers could be insufficient to provide a significant advantage compared to individual learners.

Here, we used an opaque virtual task specifically designed to generate a rugged and multidimensional fitness landscape. Adult human subjects, placed in closed groups were requested to collect a maximum weight of fish during a session of 15 trials by developing fishing nets. Three experimental conditions were run: individual learning treatment, product-copying treatment, and process-copying treatment. The efficiency of the different types of social learning was evaluated by comparing individual performances in the three treatments.

Methods

PARTICIPANTS

A total of 120 participants (64% of female) were randomly selected from a database managed by the Laboratory of Experimental Economics of Montpellier (LEEM) and recruited by e-mail from various universities in Montpellier (Southern France). The subjects ranged in age from 18 to 57 (mean = 24 years, SD = 4.9). Each participant was randomly assigned to one condition of the experiment. The participants received fees for travel according to the LEEM operating rule (2 € for local students, 6 € for others).

PROCEDURE

The experiment took place in a computer room at the LEEM. For one session, 20 players sat at a physically separated and networked computer and were randomly assigned to one group (five players per group, four groups per session). They could not see each other, and they were blind regarding the purpose of the experiment and regarding who belonged to their group. The players were instructed that communication was not allowed. The participants could read instructions on their screen about the rewards and the goal of the game, and they were requested to enter their sex and birth date before the start of the game. At the end of the game, each subject was paid in private. For each group, 50 € was distributed according to the rank of the performance of each player: 20 € for first place, 15 € for second place, 10 € for third place, 5 € for fourth place, and nothing for last place.

The rules of the game varied according to the three treatments of interest. For each treatment, eight independent groups played the game. As the duration of the game was not the same for the three treatments (see below), the groups allocated to the same treatment were run within the same session. This prevented any perturbation caused by groups finishing earlier.

GAME

Principle

The participants played a computer game (programmed in Object Pascal with Delphi6) during which they had to achieve a complex virtual task. The aim was to build a virtual fishing net to capture fish during virtual fishing trials. The number of fish captured, weighted by their size, defined the score of each fishing trial. The players had 15 trials to improve their cumulative score. To avoid artificial incentives toward exploration of the adaptive landscape, the players were not aware of the highest possible score. Each period of construction was followed by an information period, whose content varied according to each treatment (see below). The final score for each player was the cumulative score across the 15 trials.

Construction period

During the construction period (limited to 180 sec), the participants had access to several virtual tools. First, they had to choose a squared grid on which to build the net using two parameters: the number of attaching points (from 3 × 3 to 7 × 7) and the spacing between the attaching points (30 possible values), see Figure 1. Once the frame was chosen, the players had access to

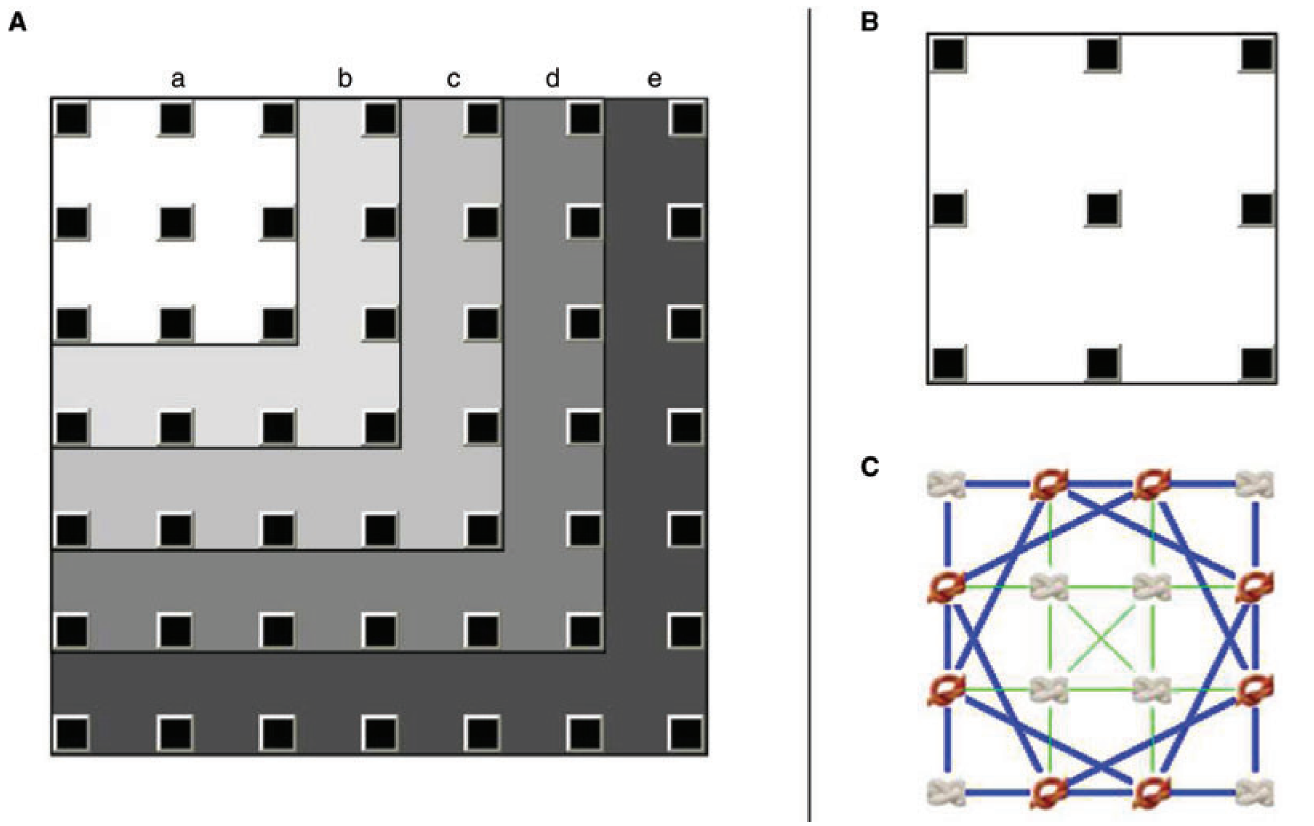

Figure 1. Parameters of net building. During the construction period, the players start by choosing the grid on which to build the net. (A) The choice of a type of grid (a, b, c, d or e) determined the number of attaching points and modified the surface on which the players built their nets. (B) Type "a" grid with modified spacing parameter. The spacing parameter modified the distance between the attaching points and the surface on which players built their nets. (C) Once the frame was chosen, the players accessed the ropes and knots to build their net. The ropes could be set between any attaching points, and the knots could be tied to any attaching points.

different types of ropes and knots. A rope could be set between any pair of attaching points, and a knot could be tied to any attaching point, in any order. There was a limited amount of ropes and knots available. Each additional rope placed on the frame decreased the length of the remaining rope quantity according to the length used. This remaining quantity was visible on the screen. There were three different types of ropes available (thick/red, medium/blue, and thin/green). Each additional knot placed on the net decreased the length of the remaining knot quantity according to the type of knot used (three sizes available). This remaining quantity of knots was visible on the screen.

During each of the 15 trials, the players could construct a new fishing net. After the first trial, they could see the net they previously constructed and the associated score, and they could also review the process in detail. Then, they had the choice to construct a new net, reuse a net, or rebuilt a net according to a process previously developed.

Construction rules

The participants were unaware of the links between the construction parameters of a net and the expected score; however, the rules were not completely arbitrary. Modification of one parameter produced complex interactions with others to generate a rugged fitness landscape (see Fig. 2). For example, the thickness of the ropes—and not the thickness of the knots—affected the expected score of the net. Additionally, the process, that is, the order of construction events, was important. Thus, two ropes that intersect at an attaching point should be tied together with a knot before another rope is put on the frame (Process Rule 1). If this step was omitted, the expected score was reduced. Similarly, if ropes of different thickness were used, the thickest rope should be placed first and the thinnest should be placed last (Process Rule 2), otherwise the expected score of the resulting net was reduced. These rules ensured that a net could not be reproduced, at least with a similar expected score, by observing only its final state.

Score calculation

Once the fishing net was constructed, it was evaluated by the program. A global resistance score (*GR*) was calculated according to the actual number of knots, and it was compared to the required number. A local resistance score (*LRi*) was determined for each

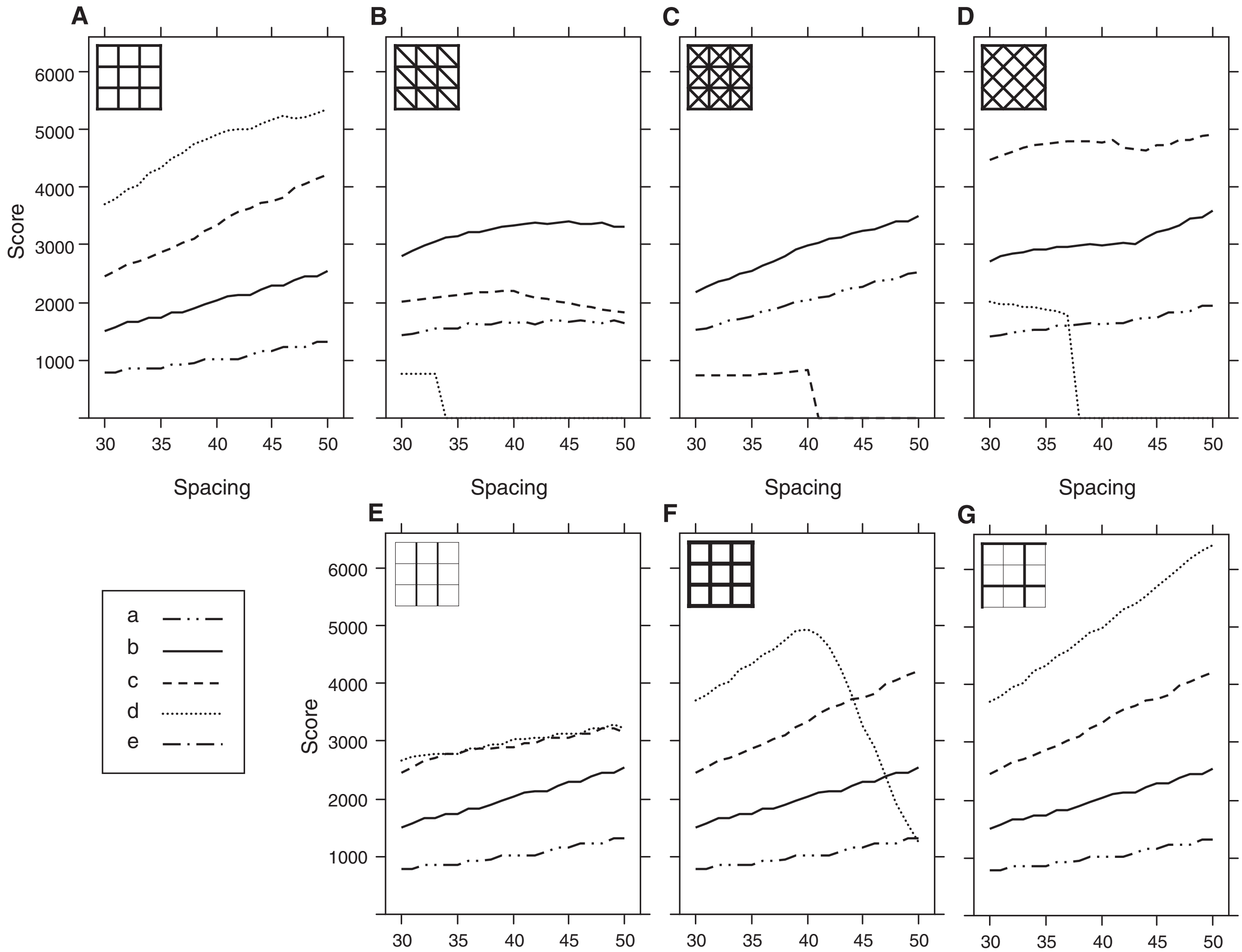

Figure 2. **Fitness landscape. An example of the expected scores for the net depicted on the top left corner of each graph (the line thickness illustrates the type of rope used) according to the spacing parameter and the type of grid (a, b, c, d, e). The pattern of the mesh (A, B, C, D) and the type of ropes (A, E, F, G) affected the fitness landscape.**

mesh i, according to the length and thickness of the ropes involved. During each virtual fishing exercise, 500 fish were launched, with a size ranging from 15 to 100 (arbitrary units). The size distribution of the fish was generated deterministically using two virtual species of different mean sizes to generate a bimodal distribution. Species 1 was smaller and fourfold more abundant than species 2. The size frequencies were: 15–30 (20%), 30–40 (70%), and 40–100 (10%) for species 1, and 15–70 (6%), 70–90 (84%), and 90–100 (10%) for species 2. The probability of each fish encountering the net increased according to the net overall size (set by the type of grid and the grid spacing) and decreased according to its visibility. The visibility of a net was computed as the sum of the length of all the ropes used, weighted by their thicknesses. Once a fish was set to interact with the net, random coordinates were generated to identify at which mesh the interaction took place. If the fish was smaller than the mesh, it escaped. If it was larger, the probability of the net breaking was calculated as $1 - (GR * LRi)$. In such a case, the whole fishing process stopped. If the net did not break, the fish could escape with a probability P_{esc}, which depends on the shape of the mesh and construction rule penalties. If the fish did not escape, its size was added to the score of the player. This process was repeated until the last fish was encountered or until the net broke.

Information period

After the period of virtual fishing, the number and size classes of the fish caught were displayed, as well as the resulting score (along with the cumulative score). The players could also see the score (and the cumulative score) of their other group members. A reminder about the importance of the process was signaled whenever a net broke or Process Rule 1 (see above) was not respected. In addition to this basic information, the players had access to supplementary social information depending on which treatment they were assigned to (see below).

TREATMENTS

The level of social information shared between the players differed according to the treatments. For the individual learning treatment, the players had access only to the last trial and the cumulative scores of each of their other group members. For the product-copying treatment, the players could see a list of the different scores of each of their group members. By clicking on the scores, the participants could see an image of the corresponding net. The participants could see an unlimited number of nets during the time of the information period, although there was no incentive to do so. For the process-copying treatment, by clicking on the scores, the participants could see the step-by-step process for building the corresponding net. The duration of the social information period was 30 sec for the individual learning treatment and 90 sec for the two other treatments.

SIMILARITY RATINGS

To quantitatively assess the differences/similarities between the fishing nets that were produced, two types of measures were used: one focusing on the visual product and one focusing on the process of construction.

Product similarity

Image analysis was used to compare the visual aspect of two nets. A method was developed to allow many pairwise comparisons and compute a measure of similarity. For nets possessing the same number of attaching points, a normalized reconstruction of each net was performed, using its original process, with some modifications: the spacing parameter was standardized, as well as the rope thickness (the color was not changed). The two nets were then scanned pixel by pixel, and two values were computed: one representing the number of shared pixels considering the rope color (absolute distance value *AV*) and one ignoring the rope color (restricted distance value *RV*). After normalization with the total sum of the pixels, the distance varied between $D_{AV} = 0$ (or $D_{RV} = 0$) for completely distinct nets and $D_{AV} = 1$ (or $D_{RV} = 1$) for exactly similar nets. Thus, for one comparison, three values were available: D_S (difference between the real spacing parameters of the two nets), D_{AV} and D_{RV}. For nets possessing different numbers of attaching points, two distinct transformations were applied sequentially on the smallest net: dilatation (T_d) and reproduction of the mesh pattern (T_r). The transformation providing the maximal D_{AV} after the pixel-by-pixel comparison was retained. Thus, for one pair comparison, the following values were available: D_S, D_{NAP} (difference in the number of attaching points of the two nets), D_{AV}, and D_{RV}.

From nets produced during a pilot experiment (independent of the main experiment), 70 pairwise comparisons involving 140 nets were run. For these same 70 comparisons, which were randomly ordered, 32 independent judges provided a similarity mark. Half of these marks (randomly selected) were used to estimate the weights α_1, α_2, β_1, β_2, δ_1, δ_2, λ that maximized the correlation between *N* and the rater values according to formula (1) or (2) (depending on whether the comparison involved nets with the same number of attaching points). The other half were used to measure this correlation ($r = 0.75$, $n = 70$, $P < 0.0001$) using the previously estimated weights.

$$N = \beta_1 \cdot D_{RV} + (1 - \beta_1) \cdot D_{AV} \cdot (1 + \alpha_1 \cdot D_S) \qquad (1)$$

$$N = (\beta_2 \cdot D_{RV} + (1 - \beta_2) \cdot (\delta_i \cdot D_{AV}) \cdot (1 + \alpha_2 \cdot D_S)) \times (1 + \lambda \cdot D_{NAP}) \qquad (2)$$

with $i = 1$ when the T_d transformation provided the minimal D_{AV} and $i = 2$ otherwise.

Process similarity

The process of each net included a succession of actions. Considering each action as a character and the succession of actions as a string, the process similarity between two nets is equivalent to the similarity between two strings. The distance between two strings was measured using the Levenshtein distance (Levenshtein 1966). This distance (D_p) was normalized with the total string length, and it varied between 0 (identical strings) and 1 (maximally distinct strings). Therefore, $1 - D_p$ provided a measure of similarity between two processes.

STATISTICAL ANALYSIS

Individual performance

The response variable was either the cumulative individual score or the highest score throughout all trials. The dependent variables were the type of learning (treatment), individual characteristics (age, sex), and group identity. Groups were considered as random samples from a larger population of interest, and thus they were introduced as a random-effect variable. Therefore, linear mixed models were used.

Social learning strategies

The response variable was the number of observed nets during each trial. The analysis was performed independently for each treatment. The dependent variables were the trial number, the squared trial number, the rank of the player in his group, individual characteristics (age, sex), and individual identity (random-effect); linear mixed models were used. The ranks of observed nets and nonobserved nets were compared using multiple Mann–Whitney–Wilcoxon tests.

Conservatism

The response variable was the conservatism variable, computed as the difference, at each trial and for each individual, between the current net and the net used in the previous trial. The dependent

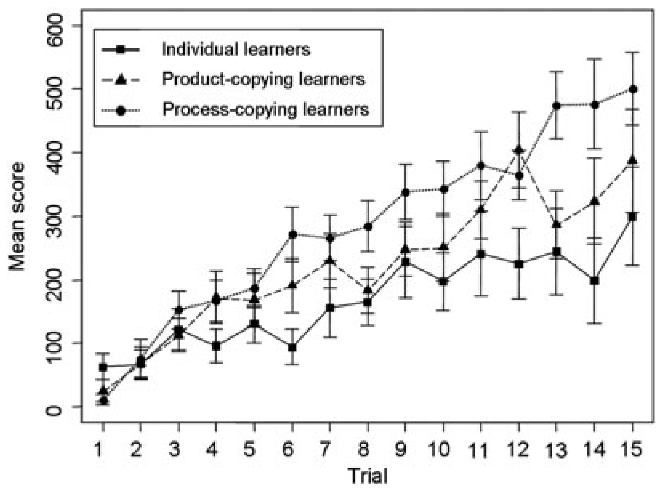

Figure 3. Mean score. Individual learners, product-copying learners, and process-copying learners improved their score throughout the 15 trials. Error bars show the standard error.

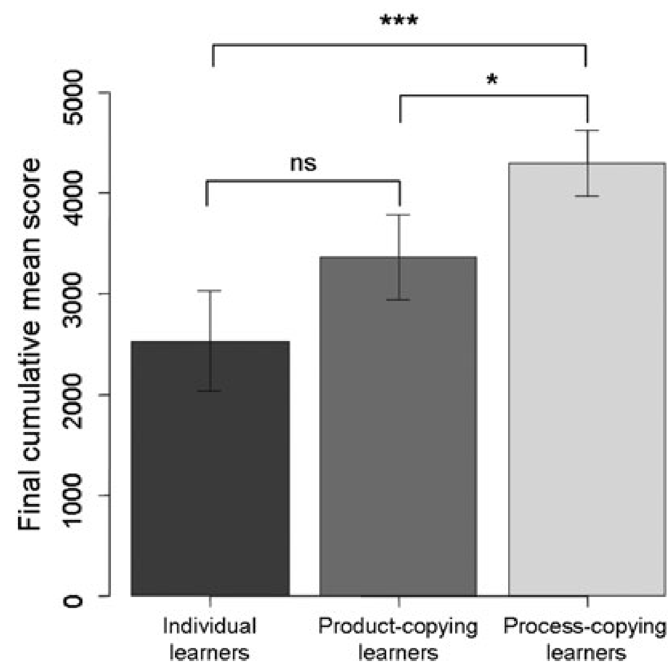

Figure 4. Final cumulative mean score. Individuals from process-copying groups outperformed individuals from product-copying groups and individual learners. Access to product information was not a sufficient condition to provide a significant advantage to social learners, compared to individual learners. Error bars show standard error.

variables were the type of learning (treatment), trial, score, the rank of the player in his group, and the change of this rank from the previous trial, as well as individual characteristics (age, sex), and individual identity (random-effect); linear mixed models were used.

Convergence

For each treatment, all possible within-group pairs ($n = 80$) and all possible between-group pairs ($n = 700$) were compared using the two similarity measures. The response variable was one or the other of these similarity measures. The dependent variables were the type of learning (treatment), the type of comparison (within-group/between-group) and the identity of each net (random-effect) in each pair. All statistical analyses were carried out using the software R 2.14.0 (R Development Core Team, 2011).

Results

TYPE OF LEARNING AND INDIVIDUAL PERFORMANCE

During the first trial, most players (86.7%) failed to build a functional net. During the following trials, functional nets were built, and the scores improved throughout the 15 trials for all treatments (individual learning: $F_{1,589} = 38.5, P < 0.0001$); product-copying, $F_{1,589} = 78.8$, $P < 0.0001$; process-copying, $F_{1,589} = 230.4$, $P < 0.0001$), see Figure 3. The number of trials before the first functional net was built (mean = 3.5) did not differ among the treatments ($F_{2,21} = 1.14$, $P = 0.34$). The individual cumulative scores were analyzed. The age of the participants had a significant effect on the cumulative score ($F_{1,94} = 7.46$, $P = 0.008$), and younger players showed a superior performance over older ones. The sex of the participants had no significant effect on their performance ($F_{1,94} = 2.30$, $P = 0.13$). Age and sex were retained in the models during the subsequent analyses.

The type of learning (treatment) had a significant effect ($F_{2,21} = 9.27$, $P = 0.001$). The comparison shows that process-copying provides a significant advantage compared to individual learning (Tukey post hoc comparison, $P < 0.001$) and product-copying (Tukey post hoc comparison, $P = 0.03$). The difference between product-copying and individual learning was not significant (Tukey post hoc comparison, $P = 0.16$), see Figure 4.

Similar trends were obtained when the highest score was analyzed instead of the cumulative score. The treatment had a significant effect ($F_{2,21} = 6.89$, $P = 0.005$), with a significant difference between process-copying and individual learning (Tukey post hoc comparison, $P = 0.0006$), a marginal but nonsignificant difference between process-copying and product-copying (Tukey post hoc comparison, $P = 0.09$), and no significant difference between product-copying and individual learning (Tukey post hoc comparison, $P = 0.22$). Finally, the highest score achieved by the best performing individual of each group did not differ significantly between treatments ($F_{2,21} = 0.97$, $P = 0.4$).

SOCIAL LEARNING STRATEGIES

In the product-copying treatment, players had access to an image of the nets designed by other group members. The number of nets inspected first increased across trials and then decreased, as shown by a significant quadratic effect (linear positive effect: $F_{1,517} = 75.5, P < 0.0001$, quadratic negative effect: $F_{1,517} = 63.0, P < 0.0001$). In addition, copying was not performed randomly within each group, as the relative position of the player in his group had a significant effect ($F_{1,517} = 13.73, P = 0.0002$). Individuals with lower ranks, that is, those who were relatively less successful, made a greater use of social information. Social learners were free to switch from one net to another so that the observation time for a given net was variable. The score of the net had a significant effect on the duration of observation ($F_{1,1316} = 235.6, P < 0.0001$), with players spending more time watching an effective net than a poor one. Finally, the nets were not observed randomly, as a net with a higher score had a higher probability of being observed by individuals (Wilcoxon–Mann–Whitney, $P < 0.01$ for each trial from Trial 3).

In the process-copying treatment, players had access to the construction details of the net designed by other group members. The number of nets inspected for their process increased during the game, and then decreased, as shown by a significant quadratic effect (linear positive effect: $F_{1,517} = 5.11, P = 0.02$, quadratic negative effect: $F_{1,517} = 4.63, P = 0.03$). Process-copying was not performed randomly within each group, as the relative position of the player in his group had a significant effect ($F_{1,517} = 5.03, P = 0.02$), with lower ranked individuals, that is, those who were relatively less successful, making a more frequent usage of social information. Finally, each process was not observed randomly, as a process with a higher score had a higher probability of being observed (Wilcoxon–Mann–Whitney, $P < 0.001$ for each trial from Trial 2).

CONSERVATISM

During each trial, the players could use their previous net or decide to build a new one. In any case, if the net at the next trial was almost similar to the previous one, then the player presented a conservative behavior. The degree of conservatism could be quantified by measuring the difference between the previous and the next net. The difference between two nets could be measured based on their final products or based on their processes.

Concerning the product, the age and sex of the players had no significant effect on the conservatism ($F_{1,115} = 1.23, P = 0.27$ and $F_{1,115} = 0.55, P = 0.45$, respectively). Overall, players were more conservative as the game progressed ($F_{1,1425} = 76.9, P < 0.0001$). Conservatism was preferred when the score of the previous trial was a success ($F_{1,1425} = 74.2, P < 0.0001$), and anticonservatism was observed when the rank of the player had decreased since the previous trial ($F_{1,1425} = 12.7, P < 0.001$). The treatment had a significant effect on conservatism ($F_{2,115} = 5.04, P < 0.001$) due to the higher conservatism of the players in the process-copying treatment than in the individual learning treatment (Tukey post hoc comparison, $P = 0.005$). A player's conservatism increased as his/her rank in his/her group increased, although this trend was not significant ($F_{1,1425} = 3.05, P = 0.08$).

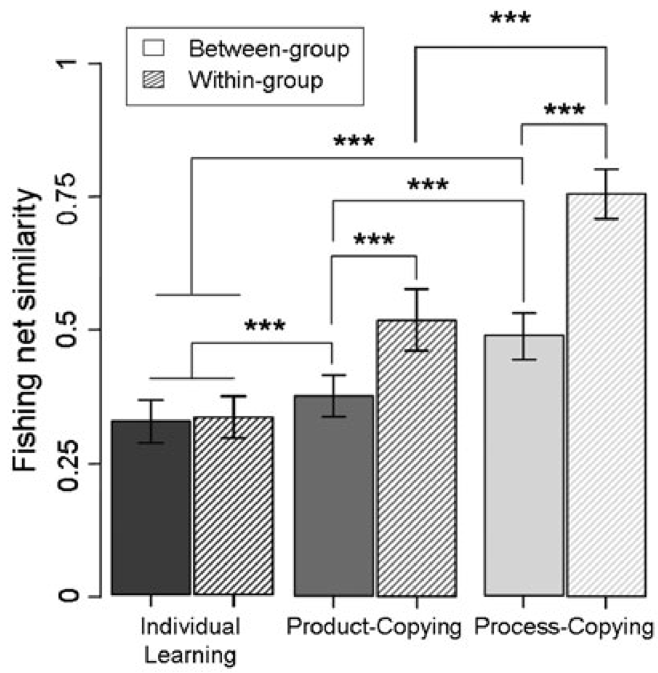

Figure 5. Within- and between-group similarity for individual learning, product-copying, and process-copying treatments. In each treatment, the similarity of the nets was measured in all possible within-group pairs (n = 80, filled bars) and all possible between-group pairs (n = 700, hatched bars).

Concerning the process, age had a significant negative effect on conservatism ($F_{1,115} = 5.16, P = 0.03$), and sex had no significant effect ($F_{1,115} = 0.68, P = 0.41$). Players became more conservative across trials ($F_{1,1432} = 110.2, P < 0.0001$), and success reinforced this behavior ($F_{1,1432} = 114.9, P < 0.0001$). Players with a higher rank were more conservative ($F_{1,1432} = 10.9, P = 0.001$), while a drop in their ranking led (nonsignificantly) the players to change their behavior ($F_{1,1432} = 2.70, P = 0.1$). Finally, the treatments showed no effect on conservatism regarding the process ($F_{2,115} = 1.83, P = 0.17$).

CULTURAL CONVERGENCE

Convergence between nets was first analyzed using product similarity. In the individual learning treatment, the within-group convergence and between-group convergence were not significantly different ($F_{1,770} = 0.14, P = 0.7$). In the product-copying and process-copying treatments, nets from the same group were more similar than nets from distinct groups ($F_{1,778} = 22.0, P < 0.0001$ and $F_{1,778} = 88.9, P < 0.0001$, respectively), see Figure 5. However, within-group cultural convergence was stronger when the social information was greater, as suggested by a significantly greater product convergence in the process-copying treatment, compared to the product-copying treatment ($F_{1,158} = 31.2$, $P < 0.0001$). Interestingly, convergence between groups in the individual learning treatment was significantly lower than in both the product-copying and the process-copying treatments ($F_{1,1470} = 27.9$, $P < 0.0001$ and $F_{1,1470} = 241.3$, $P < 0.0001$, respectively), illustrating a between-group cultural convergence when social information was available. This convergence was significantly stronger in the process-copying treatment than the product-copying treatment ($F_{1,1398} = 111.1$, $P < 0.0001$).

Concerning the process, in the individual learning treatment, the within-group convergence and between-group convergence were not significantly different ($F_{1,778} = 0.30$, $P = 0.58$). In the product-copying treatment, the processes within the same group were marginally more similar than those from distinct groups ($F_{1,778} = 3.02$, $P = 0.083$). In the process-copying treatment, processes within the same group were significantly more similar than those from distinct groups ($F_{1,778} = 133.3$, $P < 0.0001$).

The between-groups convergence in the process-copying treatment was significantly greater than in the individual learning and product-copying treatments ($F_{1,478} = 193$, $P < 0.0001$ and $F_{1,1398} = 257$, $P < 0.0001$, respectively), whereas no difference was observed between the individual learning and product-copying treatments ($F_{1,778} = 1.27$, $P = 0.26$).

Discussion

The present experiment was based on an opaque virtual task, that is, the process allowing the construction of an efficient item was not deductible from the object. The results show that individuals from process-copying groups outperformed individuals from product-copying groups or individual learners, whereas access to product information was not a sufficient condition for providing an advantage to product-copiers. When a social learner visually inspects the net of a competitor (product-copying treatment), the information collected is necessarily incomplete. This missing information is crucial to the learners, making the information collected of little use. In contrast, process-copying learners, having access to the complete information, are able to construct an equally efficient copy. Contrary to what the current models suggest (Boyd and Richerson 1995; Rogers 1988), here the use of social information does not hamper population progress at the group level. Under particular spatial structure, the strategy of pure social learner can also increase the average fitness of individuals (Rendell et al. 2010), but here no spatial structure was introduced. In our experiment, there was most likely no drop of fitness landscape exploration in the groups of social learners, as the highest score of the best performing individual in each group did not differ across treatments. The incentive of the present game was the cumulative score over all of the fishing trials. When the incentive is the highest score, as was observed by Mesoudi (2008), an opportunity exists for a wider exploration of the fitness landscape at a lower cost, thus encouraging the exploration of the fitness landscape. The emphasis on the cumulative score (rather than the highest score) corresponds to situations where there is a trade-off between winning resources in a safe way (exploring a local and known optimum) and taking the risk of losing it (to win more). Further, individual and efficient exploration of a rugged landscape (as here) is not straightforward, and a combination between a rugged fitness landscape and a trade-off related to exploration could lead individual learners to minimize their exploration, offering an advantage to strategies relying on additional information, that is, social learning.

The results about conservatism, the propensity that an individual will repeat his previous behavior rather than produce a different behavior, support this view. For all treatments, the individuals became more conservative during the 15 trials. As the game proceeded, the players improved their fishing outcome compared to the first attempts, and thus identified some successful solutions. As any change was then most likely risky, the players became more conservative, reducing their exploration of the fitness landscape. Further, the result shows that the treatment did not affect conservatism, suggesting that social learning did not reduce the exploration of the fitness landscape. As described above, the design of the experiment requires the players face a trade-off between conservatism (allowing the collection of an expected value) and change (allowing the potential to earn more at the risk of earning less). This trade-off was operating for both individual and social learners, although risk taking was most likely reduced for social learners due to their use of social information to orient change.

An exception, about conservatism, concerns the comparison between individual learners and process-copiers about product similarity. The stronger conservatism observed in process-copiers compared to individual learners could result from the cultural convergence observed within groups of social learners. Indeed, within-group cultural convergence was present for social learners, that is, nets from individuals from the same group were more similar than nets from distinct groups. This cultural convergence could represent a (local) limit to cultural evolution. Indeed, if social learning leads the majority of a group to adopt a particular behavior (as was observed here), then conformism, the tendency to follow the majority, opposes change and innovation (Whitehead and Richerson 2009). Between-group convergence was also found, despite the fact that the groups were completely independent. Interestingly, this convergence concerns a suboptimal fishing net shape (see Fig. 2C for the fitness landscape associated with most common mesh of the experiment), suggesting that social learning somehow directed cultural evolution.

This type of convergence has been reported previously (Caldwell and Millen 2008), thus suggesting that it is most likely a general phenomenon. There are various possible types of cognitive constraints that may orient cultural evolution (such as the mental representation, Sperber 1996), although more work is needed to understand this phenomenon.

Finally, it is worth noting that social learners use complex social learning strategies and that the use of strategies is commonly considered as a means to avoid the cost of social learning at the group level (Feldman et al. 1996; Kameda and Nakanishi 2002, 2003; Enquist et al. 2007). For example, when several fishing nets were available for inspection, the players did not focus on the best one; rather they screened a large number of them. This strategy is thought to be beneficial because individuals that observe group members can obtain more accurate information and thus make better-informed decisions on the basis of the most reliable information available (van Bergen et al. 2004). Individuals could also seek redundancy, as social reinforcement from multiple sources reduces uncertainty and seems to be a strong behavioral determinant (Centola 2010; Morgan et al. 2012). Apparently, after a massive inspection of fishing nets, the use of social information subsequently dropped during the last part of the game. This decrease could result from the difficulty of processing the information from a growing number of sources (Jacoby et al. 1974). Alternatively, the within-group convergence observed during the trials introduced an information redundancy among the available fishing nets, making the inspection of large number of items useless. Several learning strategies, which have been described in the literature (Laland 2004), were also observed here, such as *copy-when-unsuccessful* (social information was used more frequently for unsuccessful players) and *copy-the-most-successful-behavior* or *pay-off biased social learning* (copying was oriented toward the more successful artifacts of the population).

Our result about the difference in terms of efficiency between product-copying and process-copying contradicts a previous study based on a task involving building a paper airplane, concluding that process-copying and product-copying learning are equally efficient (Caldwell and Millen 2009). However, building a paper plane is a game that most likely every occidental child has already practiced, thus the simple view of the product is probably sufficient to emulate, at least partially, the previous knowledge of construction steps. Therefore, a paper airplane could not be considered as a truly opaque object for most occidental individuals. The importance of process-copying for efficient information transmission between individuals has important implications for understanding cumulative cultural evolution, usually described as the capacity to accumulate modifications from different individuals over time (Boyd and Richerson 1996; Tomasello 1999). Indeed, it was argued that most human artifacts are more or less opaque, even in relatively simple material cultures such as those of hunter gatherers (Ohmagari and Berkes 1997), suggesting that cumulative cultural evolution require process-copying ability. The absence of cumulative culture in other species most likely cannot be only explained by the specific human learning abilities, as these cognitive skills are derived, that is, they have probably coevolved with the material culture. The initial conditions for the evolutionary emergence of cumulative culture could also depend on various factors such as population structure (Rendell et al. 2010) or cognitive skills (Stout 2011). However, as the capacity to process-copying is unique to humans (Horner and Whiten 2005; Tennie et al. 2009 but see Whiten et al. 2009) plausibly this ability held a key role in the evolution of the cumulative culture (Boyd and Richerson 1996; Tomasello 1999; Tennie et al. 2009). Recent cumulative culture experiments support this view by suggesting that the success of children, compared to apes and monkeys, is strongly associated with a package of sociocognitive processes, including teaching, imitation, and prosociality (Dean et al. 2012).

ACKNOWLEDGMENTS

We thank C. Faurie for useful comments, R. Belkhir for help in the establishment of the SQL database, D. Dubois for recruiting students and organizing the experimental sessions, A. Comte for help during the experiment, and O. Gimenez for statistical advices. Contribution ISEM 2012-125.

LITERATURE CITED

Boyd, R., and P. J. Richerson. 1995. Why does culture increase human adaptability. Ethol. Sociobiol. 16:125–143.

———. 1996. Why culture is common, but cultural evolution is rare? Proc. Br. Acad. 88:77–93.

Caldwell, C. A., and A. E. Millen. 2008. Experimental models for testing hypotheses about cumulative cultural evolution. Evol. Hum. Behav. 29:165–171.

———. 2009. Social learning mechanisms and cumulative cultural evolution: is imitation necessary? Psychol. Sci. 20:1478–1483.

Centola, D. 2010. The spread of behavior in an online social network experiment. Science 329:1194–1197.

Dean, L. G., R. L. Kendal, S. J. Schapiro, B. Thierry, and K. N. Laland. 2012. Identification of the social and cognitive processes underlying human cumulative culture. Science 335:1114–1118.

Efferson, C., R. Lalive, P. J. Richerson, R. McElreath, and M. Lubell. 2008. Conformists and mavericks: the empirics of frequency-dependent cultural transmission. Evol. Hum. Behav. 29:56–64.

Enquist, M., K. Eriksson, and S. Ghirlanda. 2007. Critical social learning: a solution to Rogers's paradox of nonadaptive culture. Am. Anthropol. 109:727–734.

Feldman, M. W., K. Aoki, and J. Kumm. 1996. Individual versus social learning: evolutionary analysis in a fluctuating environment. Anthropol. Sci. 104:209–231.

Giraldeau, L. A., T. J. Valone, and J. J. Templeton. 2002. Potential disadvantages of using socially acquired information. Philos. Trans. R. Soc. Lond. B 357:1559–1566.

Heyes, C. M. 1994. Social-learning in animals—categories and mechanisms. Biol. Rev. 69:207–231.

Horner, V., and A. Whiten. 2005. Causal knowledge and imitation/emulation switching in chimpanzees (Pan trogiodytes) and children (Homo sapiens). Anim. Cogn. 8:164–181.

Jacoby, J., D. E. Speller, and C. A. Kohn. 1974. Brand choice behavior as a function of information load. J. Market Res. 11:63–69.

Kameda, T., and D. Nakanishi. 2002. Cost-benefit analysis of social/cultural learning in a nonstationary uncertain environment—an evolutionary simulation and an experiment with human subjects. Evol. Hum. Behav. 23:373–393.

———. 2003. Does social/cultural learning increase human adaptability? Rogers's question revisited. Evol. Hum. Behav. 24:242–260.

Laland, K. N. 2004. Social learning strategies. Learn. Behav. 32:4–14.

Levenshtein, V. I. 1966. Binary codes capable of correcting deletions, insertions, and reversals. Sov. Phys. Dokl. 10:707–710.

McElreath, R., M. Lubell, P. J. Richerson, T. M. Waring, W. Baum, E. Edsten, C. Efferson, and B. Paciotti. 2005. Applying evolutionary models to the laboratory study of social learning. Evol. Hum. Behav. 26: 483–508.

Mesoudi, A. 2008. An experimental simulation of the "copy-successful-individuals" cultural learning strategy: adaptive landscapes, producer-scrounger dynamics, and informational access costs. Evol. Hum. Behav. 29:350–363.

Morgan, T. J. H., L. E. Rendell, M. Ehn, W. Hoppitt, and K. N. Laland. 2012. The evolutionary basis of human social learning. Proc. R. Soc. Lond. B 279:653–662.

Ohmagari, K., and F. Berkes. 1997. Transmission of indigenous knowledge and bush skills among the Western James Bay Cree women of subarctic Canada. Hum. Ecol. 25:197–222.

Oswalt, W. H. 1976. An anthropological analysis of food-getting technology. Wiley, New York.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at http://www.R-project.org/.

Rasmussen, K. 1908. The people of the Polar north. Kegan Paul, Trench, Trubner & Co., London.

Rendell, L., L. Fogarty, and K. N. Laland. 2010. Rogers' paradox recast and resolved: population structure and the evolution of social learning strategies. Evolution 64:534–548.

Rogers, A. R. 1988. Does biology constrain culture? Am. Anthropol. 90:819–831.

Sperber, D. 1996. Explaining culture: a naturalistic approach. Blackwell, Oxford, U.K.

Stout, D. 2011. Stone toolmaking and the evolution of human culture and cognition. Philos. Trans. R. Soc. Lond. B 366:1050–1059.

Tennie, C., J. Call, and M. Tomasello. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. Lond. B 364:2405–2415.

Tomasello, M. 1999. The cultural origins of human cognition. Harvard Univ. Press, Cambridge, U.K.

van Bergen, Y., I. Coolen, and K. N. Laland. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proc. R. Soc. Lond. B 271:957–962.

Whitehead, H., and P. J. Richerson. 2009. The evolution of conformist social learning can cause population collapse in realistically variable environments. Evol. Hum. Behav. 30:261–273.

Whiten, A., N. McGuigan, S. Marshall-Pescini, and L. M. Hopper. 2009. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. Philos. Trans. R. Soc. Lond. B 364:2417–2428.

Associate Editor: S. West