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# How does competition affect the transmission of information? $\stackrel{\scriptstyle\scriptstyle\swarrow}{\sim}$

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#### ABSTRACT

The use of social information is a prerequisite to the evolution of culture. In humans, social learning allows individuals to aggregate adaptive information and increase the complexity of technology at a level unparalleled in the animal kingdom. However, the potential to use social information is related to the availability of this type of information. Although most cultural evolution experiments assume that social learners are free to use social information, there are many examples of information withholding, particularly in ethnographic studies. In this experiment, we used a computer-based cultural game in which players were faced with a complex task and had the possibility to trade a specific part of their knowledge within their groups. The dynamics of information transmission were studied when competition was within- or exclusively between-groups. Our results show that between-group competition improved the transmission of information, increasing the amount and the quality of information. Further, informational access costs did not prevent social learners from performing better than individual learners, even when between-group competition was absent. Interestingly, between-group competition did not entirely eliminate access costs and did not improve the performance of players as compared with within-group competition. These results suggest that the field of cultural evolution would benefit from a better understanding of the factors that underlie the production and the sharing of information.

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#### 1. Introduction

The ability to gather and use information provided by the behaviors of others, namely social learning, is a prerequisite for the evolution of culture. From an evolutionary perspective, the use of social information is commonly considered to be profitable because it allows the avoidance of the costs of trial-and-error-learning in terms of the effort and risks (Boyd & Richerson, 1985). Experimental studies have shown that humans use social information in many manners and under various conditions (Mesoudi, 2011; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). The particularly developed human capacity to learn socially allows information to flow between individuals, which results in an accumulation of adaptive information. Consequently, humans possess a complex technology that no individual could possibly invent alone (Boyd & Richerson, 2005).

However, the possibility to use social information is closely related to its availability. From the perspective of the copied individuals (designated as models), social learners are parasites because they exploit information without contributing new information themselves (Kameda & Nakanishi, 2002; Laland, 2004; Rogers, 1988). Thus,

1090-5138/\$ - see front matter © 2014 Elsevier Inc. All rights reserved. http://dx.doi.org/10.1016/j.evolhumbehav.2013.11.001 models are most likely reluctant to share information unless they have an incentive to share. One may object that many behaviors can be copied by simple visual contact without implying close proximity to the models. However, even in relatively simple material cultures, such as those of hunter–gatherers, the processes or skills that allow the construction of an item are generally not readily deduced from the object itself (Ohmagari & Berkes, 1997). In this case, the opacity of the objects prevents social learners from constructing an equally efficient copy using simple visual contact (Acerbi, Tennie, & Nunn, 2010; Derex, Godelle, & Raymond, 2013).

There are many ethnographic examples of information withholding, oriented sharing or secrecy for all types of information. For instance, among the adze makers in the village of Langda in Indonesian Irian Jaya, the craftsmen report that they instruct only close relatives because of the great value of the skill (Stout, 2002). Additionally, among the Asabano from Papua New Guinea, older men enjoy the status associated with religious knowledge and control its oral dissemination (Lohmann, 2001). More generally, ethnographic studies suggest that information is commonly treated as a good, which is traded between models and learners, with low-status individuals giving gifts or deference to high-status individuals in exchange for their expert knowledge (Henrich & Gil-White, 2001).

The wide majority of cultural evolution studies assume that cultural learners are free to use social information (Caldwell & Millen, 2008; Kameda & Nakanishi, 2002; Kameda & Nakanishi, 2003; Kempe, Lycett, & Mesoudi, 2012; Mesoudi, 2011). However, a more

 $<sup>\</sup>stackrel{\uparrow}{\times}$  Raw data are included as Supplementary Material (available on the journal's website at www.ehbonline.org).

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realistic setting would be to allow models to impose costs in exchange for information. Only one study has looked at the consequence of allowing informational access cost (Mesoudi, 2008). In this experiment, players had to virtually design an arrowhead by the modification of 5 attributes and were allowed to set access costs that other participants had to pay them in order to view their arrowhead design. Under this setting, successful players tend to offer their information only for a high price, thus preventing other group members from socially collecting useful information (Mesoudi, 2008). A consequence of this restricted information access is to prevent the transmission of the adaptive information necessary for the evolution of cumulative culture and make social learners unable to invade the population.

It has been suggested that the uniquely human form of cooperation has played a fundamental role in human cultural evolution (Tennie, Call, & Tomasello, 2009). Humans cooperate in large groups with non-kin, even strangers, and this characteristic may substantially increase the number of transmission events among individuals. However, cooperation is not operating in every case, even if two individuals have potentially mutual benefits (e.g., by trading knowledge versus a gift). In humans, it has been shown, analytically and experimentally, that cooperation is affected by the scale of competition (West et al., 2006). Indeed, with local competition, fitness is relative to social partners, and cooperation benefits social partners. Thus, in Mesoudi's experiment (Mesoudi, 2008), most likely players had no incentive to share their information as they were in direct competition with their group members. In contrast, betweengroup competition favors individually costly, group-beneficial behaviors, such as cooperation and altruism (Bowles, 2006; Boyd, Gintis, Bowles, & Richerson, 2003; Darwin, 1871; Frank, 2003; Roes & Raymond, 2003). Indeed, in this case, specific conditions unite the interest of individuals and make the group more cohesive. For example, in the extreme case in which individuals cannot compete against other group members, each individual can increase its own success only by increasing the efficiency and productivity of the entire group.

The individual's possibility of conserving an advantage following the transmission of information could also improve the transmission of information. In Mesoudi's experiment, successful players had no choice to deliver partial or old information (Mesoudi, 2008): following the sharing of information, the model and the learner possess the same information, so that the model's advantage is reduced to the price of the transaction. Further, information holders (the model plus the learner) will be in competition to trade the same information, thereby reducing the value of information. Under this setting, successful individuals most likely had no incentive to share their information. However, opacity of material culture could allow more complex sharing strategies: as opacity of cultural artifacts prevents social learners from constructing an equally efficient copy using visual contact, successful individuals could trade their products, keeping the process (allowing to produce products) for themselves. More generally, individuals' strategies can be more complex than choosing between sharing and not sharing: due to the nature of cultural information, models could exhibit many subtle strategies such as delayed or partial transmission. With the possibility to withhold some information, models could share information with learners (with mutual benefits) without endangering themselves.

The aims of this study were (1) to investigate how betweengroup competition affects the transmission of information, (2) to examine if social learners with access costs outperform individual learners only when the competition is between groups. A complex virtual task was proposed to players with the possibility of trading their information within their group. Two treatments were considered, in which competition was either within or between groups. In all cases, players had the possibility of trading specific portions of their knowledge.

#### 2. Methods

#### 2.1. Participants

A total of 120 participants (64 women) were randomly selected from a database managed by the Laboratory of Experimental Economics of Montpellier (LEEM) and were recruited by email from various universities in Montpellier (Southern France). The subjects ranged from 18 to 36 years old (mean = 23 years, s.d. = 3.0). Each participant was randomly assigned to one of the two conditions of the experiment. The participants received travel fees according to the LEEM operating rule ( $2 \in$  for local students,  $6 \in$  for others).

#### 2.2. Procedure

The experiment occurred 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 (5 players per group, 4 groups per session). The participants could not see one another and were blind regarding the purpose of the experiment and who belonged to their group. The players were instructed that communication was not allowed. The participants could read instructions on their screen regarding the rewards and goals of the game and were requested to enter their sex and birth date before the beginning of the game. The specified aim of the game depended on which of the treatments was tested (within-group competition or between-group competition, see 2.4. Treatments).

#### 2.3. Game

#### 2.3.1. Principle

The participants played a computer game (programmed in Object Pascal with Delphi 6) during which they had to achieve a complex virtual task. The aim was to construct a virtual fishing net to capture fish during virtual fishing trials. The number of fish captured and weighed by size defined the score for each trial. The players had 15 trials to improve their cumulative score. Each period of construction was followed by a transaction period, in which the content varied according to each treatment (see below). The final score of the player was their cumulative score across 15 trials plus the balance (positive or negative) associated with the purchases and sales performed by the player.

#### 2.3.2. Construction period

During the construction period (limited to 180 s), 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  $3 \times 3$  to  $7 \times 7$ ) and the spacing between the attaching points (see (Derex et al., 2013) for complete details). Once the frame was chosen, the players had access to 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 were three different types of ropes available (thick/red, medium/blue and thin/green), and three different types of knot.

During each of the fifteen trials, the players could construct a new fishing net; in this case, the manufactured product and associated process were added to his toolbox. After the first trial, the individuals could view the net that they had previously constructed and its associated score and could also review the process in detail. Subsequently, the participants had the option to construct a new net, reuse a net from their toolbox or rebuild a net according to a previously developed process.

#### 2.3.3. 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 in order to generate a rugged fitness landscape. For example, the thickness of the ropes – and not the thickness of the knots – affected the expected score of the net. Additionally, the process, i.e. 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.

#### 2.3.4. 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 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 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 Pesc, 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.

#### 2.3.5. Transaction period

After the period of virtual fishing, the number and class sizes of the caught fish were displayed with the resulting and cumulative scores. The players could also view the scores (and cumulative scores) of the other group members. Additionally, in the between-group competition treatment (see below), the players could view the cumulative score of his own and competitor group.

Supplementary social information could be traded within a group during the transaction period. When a player constructed a net, two marketable items were generated: the product and the process. The players could establish a price for their products, processes or both, so that they could choose what they wanted to put up for sale. The prices were bound between 0 and 999,999, in the same arbitrary unit as the scores. The items put up of for sale were visible to other group members in the *products to sell* or *processes to sell* lists, and were associated with their scores. To buy an item, a player should have a cumulative score greater than (or equal to) its price. Following a purchase, the price of the item was subtracted from the cumulative score of the buyer and added to the cumulative score of the seller.

Importantly, we considered products as the actual, ready-to-use nets, and processes as the knowledge associated with the step-bystep procedure allowing building the nets. Indeed, product information, as used in the social learning mechanism literature, is an information easily available for a social learner. Thus, it is most likely unrealistic to consider that successful players could prevent learners to scrounge product information. As a consequence, in this game, players possessed the item following a purchase.

Only one individual could possess a product; when the product was sold, it was removed from the seller's toolbox and added to the buyer's toolbox. However the seller could reproduce the sold product at the next construction period if he possesses the associated process. Thus, a successful player could sell his products without reducing the value of his information, as a product sold cannot be duplicated (due to its opacity) by the buyer. A process could be sold to several customers and was also retained by the owner when sold. The duration of the transaction period was 90 s.

#### 2.4. Treatments

Two treatments were considered. For the within-group competition (WGC) treatment, the players competed with other players of their own group and traded information with their competitors. In this case, the stated objective was to maximize the individual cumulative score. For each group, 50 € was distributed according to the rank of the performance of each player:  $20 \in$  for the first,  $15 \in$  for the second,  $10 \in$  for the third,  $5 \in$  for the fourth and nothing for the fifth. For the between-group competition (BGC) treatment, a group of five players competed with another group of five players and only traded information with their co-operators. The stated objective was to maximize the group cumulative score. Each player earned 15 € if they belonged to the winning group, otherwise they received  $0 \in At$ the end of the game, each subject was paid in private. For each treatment, 8 independent games were performed, so that 40 players participated to WGC treatment  $(8 \times 5 \text{ players})$  and 80 to BGC treatment (8  $\times$  2 groups  $\times$  5 players).

#### 2.5. Statistical analyses

#### 2.5.1. Details

To simplify the interpretation, the events relating to the products and processes were analyzed separately, i.e., the below-presented analyses were repeated for both types of items, i.e. products and processes. Markov Chain Monte Carlo methods were used to fit the models (Kruschke, 2010). Contrary to the frequentist statistical approach, which estimates the value for the parameter that makes the model most consistent with the data in the sense of, e.g., minimizing the sum squared deviation, MCMC provides the range of parameter values (credible intervals) that are reasonably consistent with the data (and hence tests of whether those parameters could plausibly equal zero).

All interactions involving sex were included in the models. The models were not simplified to prevent bias associated with stepwise multiple regression (Whittingham, Stephens, Bradbury, & Freckleton, 2006), with the exception of "non-significant" interaction terms (for which the 95% credible interval included 0). The parameter values were estimated using a sample of 10,000 iterations. The estimates were reported in linear units. All statistical analyses were conducted using R 2.14.0 (R Development Core Team, 2011), using the packages Ime4 (Bates, Maechler, & Bolker, 2011) for mixed models, MCMCpack (Martin, Quinn, & Park, 2011) and languageR (Baayen, 2011) for credible intervals.

#### 2.5.2. The effect of the competition on the transmission of information

The response variable was the number of transactions that occurred within the groups. The independent variables were the type of competition (treatment), and mean age and sex ratio within the group.

#### 2.5.3. The effect of the competition on the accessibility of information

The response variable was the price of the proposed items (logtransformed). The independent variables were the type of competition (treatment) and individual characteristics (age and sex). "Individual identity" nested in "Group identity" was introduced as random factor. This factor was introduced because the players were aware of the prices proposed by the other members of their own group and because there was the potential for non-independence within the data.

#### 2.5.4. The effect of the quality of information on its accessibility

To investigate how the quality of information affected its accessibility, the analyses were performed independently for each treatment. The response variable was the price of the proposed items. The independent variables were the item performances (product score and rank within the toolbox of the player), individual performances (rank and squared rank of the player), individual characteristics (age and sex) and fishing trial. "Individual identity" nested in "Group identity" was included as random factor.

#### 2.5.5. Who benefits from information transmission?

To investigate how information flowed, the analyses were performed independently for each treatment. The dependent variables were the number of sales or purchases, or the sum of incomes or expenses. Individual performances (the mean rank and mean squared rank of the player) were introduced in the models.

#### 2.5.6. Performance

The response variable was the cumulative individual score. The independent variables were the type of learning (treatment), individual characteristics (age and sex) and "group identity" was introduced as random factor. The data for the individual learning treatment from a previous similar experiment (Derex et al., 2013) were used.

#### 3. Results

## 3.1. Does between-group competition increase the number of transactions?

Between-group competition induced an increase in effective transmission of the products and the processes, respectively an average of 4.31 and 9.02 additional transactions occurred per group from the BGC treatment compared to the groups from the WGC treatment (95% credible interval (CI): (0.07, 8.47) and CI: (2.99, 14.95), respectively). Compared to the processes, more products flowed in the WGC treatment, whereas the reverse trend was observed in the BGC treatment (WGC treatment: 49 products/40 processes (total among 8 groups); BGC treatment: 164 products/209 processes (total among 2 × 8 groups); Fisher's exact test, one-sided: P = 0.039, see Fig. 1).

## 3.2. Does between-group competition improve the accessibility of information?

Products from the BGC treatment were 1.46 linear units lower than those from the WGC treatment (CI: (-2.34, -0.66)), and the processes lower by 0.88 linear units (CI: (-1.71, -0.09)). On average the price associated with a product was 69% of its expected score in the WGC treatment, and 32% in the BGC treatment. Concerning the processes, prices were 53% of the expected score in the WGC treatment, and 47% in the BGC treatment. At the end of the game the players' expenditures reached on average 10.3% of their cumulative score in the WGC treatment, and 5% in the BGC treatment.

#### 3.3. Does the quality of information reduce its accessibility?

The performance of the items positively influenced its price in each treatment (Table 1). Further, in the WGC treatment, the price of the products increased according to the rank of the player: products from first ranked players were, on average, 20% more expensive than those from fifth ranked players. No effect of individual performance was observed in the BGC treatment. In the two treatments, the processes



**Fig. 1.** The mean number of transactions having taken place per group during the entire game for each treatment. Compared to the number of products, more processes were transmitted in the BGC treatment, whereas the reverse trend was observed in the WGC treatment (Fisher's exact test, one-sided: P = 0.039). The error bars show the standard error of the mean.

from the intermediate players were more expensive. In the WGC treatment, processes from the third ranked players were the most expensive: an increase of 9.4% as compared with first ranked player

#### Table 1

Predictor variables for the product and process prices. Medians and 95% credible intervals, as estimates of the parameter values. The bold characters indicate estimate values with a 95% credible interval not including zero. "Item" designates either a product or process.

		a) Product			b) Process		
		2.5%	97.5%	Median	2.5%	97.5%	Median
WGC	(Intercept)	2.54	3.97	3.29	-1.24	3.48	1.2365
	Age	-0.01	0.18	0.09	-0.05	0.15	0.0463
	Sex (ref = $F$ )	0.33	1.40	0.85	0.34	1.72	1.1139
	Player's rank $(Best = 1)$	-0.37	-0.10	- 0.25	-0.21	0.15	-0.0622
	Player's sq. rank	-0.18	-0.002	-0.10	-0.23	-0.02	- 0.1374
	Fishing trial	0.003	0.11	0.06	-0.03	0.11	0.0433
	Item's rank	-0.14	0.03	-0.06	-0.07	0.11	0.0231
	(Best = 1)						
	Item's score	0.001	0.002	0.0017	0.002	0.005	0.004
BGC	(Intercept)	2.76	4.66	3.66	0.95	5.47	3.4735
	Age	-0.09	0.10	0.01	-0.08	0.10	0.0118
	Sex (ref = $F$ )	-1.31	0.23	-0.51	-0.20	0.94	0.3778
	Player's rank	-0.08	0.22	0.07	-0.18	0.15	-0.0337
	(Best = 1)						
	Player's sq. rank	-0.07	0.13	0.00	-0.23	-0.01	-0.1421
	Fishing trial	-0.13	-0.02	-0.07	-0.10	-0.01	-0.0586
	Item's rank	-0.18	-0.03	-0.11	-0.15	-0.03	-0.0802
	(Best = 1)						
	Item's score	0.0003	0.001	0.0007	0.0008	0.0014	0.0011
	Age $\times$ Sex	0.09	0.47	0.28	-	-	-
	$\mathrm{Sex} \times \mathrm{Fishing}$	0.03	0.18	0.01	-	-	-
	trial						
	$\text{Sex} \times \text{Item's}$	-	-	-	-0.17	-0.0003	-0.099
	rank						

and of 15% as compared with the fifth ranked players. In the BGC treatment, processes from the third ranked players were also the most expensive: an increase of 14% as compared with first ranked player and of 18% as compared with the fifth ranked players.

#### 3.4. Who benefit from information transmission?

In the WGC treatment, the rank of the player had no effect on his number of products and processes purchased (rank: median = 0.16, CI: (-0.14, 0.45); squared rank: median = -0.15, CI: (-0.47, 0.16), and rank: median = 0.04, CI: (-0.22, 0.29); squared rank: median = -0.15, CI: (-0.42, 0.11), respectively, Fig. 2) or products and processes sold (rank: median = -0.16, CI: (-0.46, 0.13); squared rank: median = -0.01, CI: (-0.32, 0.31) and rank: median = -0.05, CI: (-0.32, 0.22); squared rank: median = 0.01, CI: (-0.20, 0.38), respectively, Fig. 3) and no effect on his expenses or incomes (details not shown). In contrast, in the BGC treatment, the worst players sold fewer products and processes (rank: median = -0.57, CI: (-0.73, -0.41); squared rank: median = 0.10, CI: (-0.06, 0.26), and rank: median = -0.68, CI: (-0.89, -0.47); squared rank: median = 0.12, CI: (-0.09, 0.33), respectively, Fig. 3) and had lower incomes (details not shown). The intermediate players were the largest buyers for the two types of items (rank: median = -0.03 CI: (-0.21, 0.14); squared mean rank median = -0.25, CI: (-0.43, -0.07), and rank: median = 0.03, CI: (-0.17, 0.23); squared rank: median = -0.24, CI: (-0.44, -0.04), respectively, Fig. 2) and the largest spenders (details not shown).

#### 3.5. Performance of the social learners

Players from the Individual Learning treatment had performances 14.8 linear units lower compared to players from the WGC treatment (CI: (-29.4, -0.92)) and 16.2 linear units lower compared to players from the BGC treatment (CI: (-29.8, -2.30), Fig. 4). No difference was observed between the players from the WGC treatment as compared to those from BGC treatment (median = 1.03, CI: (-12.8, 14.0)). The age and sex of the participants had no effect on the cumulative score (median = -0.62, CI: (-2.24, 0.64) and median = -1.13, CI: (-9.72, 7.95), respectively).



**Fig. 2.** The number of purchases according to the player's rank. In the BGC treatment, the intermediate players were the largest buyers (solid line = products; dashed line = processes). No relationship between the player's rank and number of purchases was observed in the WGC treatment. The error bars show the standard error of the mean.



**Fig. 3.** The number of sales according to the player's rank. In the BGC treatment, the best players sold more products (solid line) and processes (dashed line) than the lower-ranked players. No relationship between the player's rank and number of sales was observed in the WGC treatment. The error bars show the standard error of the mean.

#### 4. Discussion

One aim of this experiment was to study how between-group competition affects the sharing of information. Two treatments were compared: individuals of an identical group were in direct competition (WGC treatment) or shared a common interest (BGC treatment). Lower proposed prices were observed when between-group competition was present, resulting in more transactions. The type of transmitted information was also affected by treatment, as more products than processes were transmitted in WGC treatment, whereas the reverse was observed in the BGC treatment. Thus between-group competition increased the number of transactions and the quality of the transmitted information. Those results are not surprising given that between-group competition unites the interests



**Fig. 4.** The final cumulative mean score. Players from the WGC and BGC treatments outperformed individual learners (IL). Between-group competition (BGC) did not improve the performance of players as compared with within-group competition (WGC). The error bars show the standard error of the mean.

of individuals: within a group, players had the same common interest. In contrast, in WGC treatment, transmission of information advantaged direct competitors. Those results are quite in line with the cooperation literature. Indeed, it was shown that cooperation is affected by the scale of competition (West et al., 2006) and that between-group competition favors individually costly, group-beneficial behaviors, such as cooperation (Bowles, 2006; Boyd et al., 2003).

Although between-group competition promotes the transmission of information, our results show that between-group competition does not entirely eliminate access cost. This is quite surprising as in BGC treatment players had no interest to make profit from their group members. Indeed, in this treatment, there was no incentive for a high within-group rank because the game was anonymous and all groupmembers earned equally and without rank considerations. It cannot be excluded that individuals extract some advantages from their anonymous success because a higher self-perception could return intrinsic benefits (Trivers, 2000). However, it is noteworthy that humans live in an environment in which social interaction is ubiquitous: an anonymous and without-reputation game is most likely out of the range of ordinary circumstances, and it is possible that psychological mechanisms unconnected to this game are expressed.

The price of the items was positively correlated with their performance in the two treatments. Thus, the best information is less easily transmitted because its higher price makes it less attainable for learners. Associating information with high and/or prohibitive prices is thus a method to retain information. In the BGC treatment, the best players did not completely prevent transmission because they sold a larger number of items (products and processes) and enjoyed higher incomes compared to lower-ranked players. In contrast, in the WGC treatment, high ranked players did not sell more than lower-ranked players. Similar results were observed in a previous experiment (Mesoudi, 2008). The persistent correlation observed between the item performance and its price, despite the decrease in internal competition, affected the access to information. Low-level players from the BGC treatment accessed fewer items than mid-level players. This result could result from the specificities of the game because the fish were the only currency available. In real life, lower-skilled individuals in a task could be more skilled in another task, thus providing a resource to trade information with the models. Overall, the alignment of individual interests (BGC treatment) affected the availability of social information but was not sufficient to allow a free flow of information within the group.

The social learners from the WGC treatment exhibited higher performances than the individual learners from a previous similar experiment (Derex et al., 2013). The internal competition did not completely prevent social transmission because 49 product and 40 process transmissions were observed. Although the number of transmission events was lower than in the BGC treatment, the circulation of some products and processes allowed social learners from the WGC treatment to outperform individual learners. This result contradicts a previous study in which the prohibitive prices of social information did not make social learners more efficient than individual learners (Mesoudi, 2008). However, in that experiment, the players could only transmit the total amount of their knowledge without the possibility to only transmit a specific component (e.g., less efficient items, or a product without its process). In this case, the benefit of the transaction equated its price, but the post-transaction advantage of the model was null because his knowledge was now completely shared by others. Most likely, this difference was pivotal: in this study, the players could transmit some information without endangering themselves, e.g., by transmitting an old process or a product without its associated process. Under these conditions, between-group competition is not a prerequisite for cultural transmission to operate. Further, it suggests that, the possibility to use some strategies of information retention could paradoxically allow a better flow of information.

Despite the increasing number of transactions, players from BGC treatment performed no better than players from WGC treatment. Why is this so? In our experiment, BGC treatment was an extreme case in which individuals cannot compete against other group members: each individual could increase its own success only by increasing the efficiency of the group (i.e. within-group competition was theoretically totally suppressed). In humans, it was suggested that social institutions that limit competition within groups (e.g. food sharing) could promote the evolution of group-beneficial behaviors by group selection (Bowles, Choi, & Hopfensitz, 2003). However, as noted by Bowles, resource sharing may reduce individual incentives to acquire resources to be shared. Thus, the frequency of betweengroup conflict is thought to be an important factor in the evolution of altruism (Bowles et al., 2003). In BGC treatment, only two groups were in direct competition and the rank of the groups determined the individual's payoffs. Thus, if the score gap between the two groups was large enough, incitation toward innovation (as well as information sharing) was weak. On the contrary, in WGC treatment, players were paid according to their rank within their group. Thus, as the number of players was higher than the number of groups, competition was theoretically stronger in WGC than in BGC treatment. In the business enterprise sector, it was suggested that the innovation rate increases with competition (Blundell, Griffith, & van Reenen, 1999) (although this relationship could be non-linear (Aghion, Bloom, Blundell, Griffith, & Howitt, 2005)). Thus, it is possible that incentive toward innovation was globally lower in BGC treatment as compared with WGC treatment. An alternative explanation is that innovation was reduced in BGC treatment not because of the lower competition, but because of the larger use of social learning. Indeed it is suspected that social learning can inhibit the exploration of the fitness landscape (Mesoudi, 2008). Thus, the larger use of social information may have led all group members from BGC to exploit the same solution and thereby make the entire group get stuck on locally optimal but globally suboptimal peak.

#### 5. Conclusion and future directions

Our experiment shows that between-group competition improves within-group information transmission between individuals. However, between-group competition was not a strong prerequisite for cultural evolution, as social learners outperformed individual learners even if between-group competition was absent. Further, betweengroup competition did not lead to a higher individual performance as compared with players facing within-group competition.

The creation of new information, that is innovation, and their transmission within the group determine the pace of cultural evolution. This experiment suggests that both could be affected by competition, either between-group or within-group. Further studies are now needed to explore in details how competition could promote cultural evolution. Cultural evolution studies assume that cultural learners are free to use social information, while a more realistic setting is most likely to allow successful individuals to impose costs in exchange for information. Our experiment shows that the individual propensity to share information is affected by several factors including the type of competition or the quality of information. Similarly to social learning strategies, which dictate the circumstances under which individuals use social information (Laland, 2004), individuals seem to use several information sharing strategies that determine the circumstances under which individuals share their information. Most likely several factors fostering or hampering the transmission of information remain to be identified. Our understanding of cultural evolution could greatly benefit from a better understanding of the factors that underlie the sharing of information and how these factors are likely to improve or reduce the process of cultural evolution.

#### **Supplementary Materials**

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.evolhumbehav.2013.11.001.

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#### References

- Acerbi, A., Tennie, C., & Nunn, C. L. (2010). Modeling imitation and emulation in constrained search spaces. *Learning & Behavior*, 39, 104–114.
- Aghion, P., Bloom, N., Blundell, R., Griffith, R., & Howitt, P. (2005). Competition and innovation: An inverted U relationship. National Bureau of Economic Research Working Paper Series, No. 9269.
- Baayen, R. H. (2011). languageR: Data sets and functions with "Analyzing linguistic data: A practical introduction to statistics". Retrieved from. http://CRAN.R-project. org/package=languageR.
- Bates, D., Maechler, M., & Bolker, B. (2011). lme4: Linear mixed-effects models using S4 classes. Retrieved from. http://cran.r-project.org/web/packages/lme4/.
- Blundell, R., Griffith, R., & van Reenen, J. (1999). Market share, market value and innovation in a panel of British manufacturing firms. *The Review of Economic Studies*, 66, 529–554.
- Bowles, S. (2006). Group competition, reproductive leveling, and the evolution of human altruism. *Science*, 314, 1569–1572.
- Bowles, S., Choi, J. K., & Hopfensitz, A. (2003). The co-evolution of individual behaviors and social institutions. *Journal of Theoretical Biology*, 223, 135–147.
- Boyd, R., Gintis, H., Bowles, S., & Richerson, P. J. (2003). The evolution of altruistic punishment. Proceedings of the National Academy of Sciences of the United States of America, 100, 3531–3535.
- Boyd, R. P. D., & Richerson, P. J. (1985). Culture and the evolutionary process. Chicago: University of Chicago Press.
- Boyd, R., & Richerson, P. J. (2005). Not by genes alone. Chicago, IL: University of Chicago Press. Caldwell, C. A., & Millen, A. E. (2008). Experimental models for testing hypotheses about cumulative cultural evolution. Evolution and Human Behavior, 29, 165–171.
- Darwin, C. (1871). The descent of man, and selection in relation to sex. London: John Murray. Derex, M., Godelle, B., & Raymond, M. (2013). Social learners require process information to outperform individual learners. Evolution, 67, 688–697.
- 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/.

- Frank, S. A. (2003). Perspective: Repression of competition and the evolution of cooperation. *Evolution*, 57, 693–705.
- Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22, 165–196.
- Kameda, T., & Nakanishi, D. (2002). Cost–benefit analysis of social/cultural learning in a nonstationary uncertain environment – an evolutionary simulation and an experiment with human subjects. *Evolution and Human Behavior*, 23, 373–393.
- Kameda, T., & Nakanishi, D. (2003). Does social/cultural learning increase human adaptability? Rogers's question revisited. Evolution and Human Behavior, 24, 242–260.
- Kempe, M., Lycett, S., & Mesoudi, A. (2012). An experimental test of the accumulated copying error model of cultural mutation for Acheulean handaxe size. *PLoS ONE*, 7, e48333.
- Kruschke, J. K. (2010). What to believe: Bayesian methods for data analysis. Trends in Cognitive Sciences, 14, 293–300.
- Laland, K. N. (2004). Social learning strategies. Learning & Behavior, 32, 4-14.
- Lohmann, R. I. (2001). Introduced writing and Christianity: Differential access to religious knowledge among the Asabano. *Ethnology*, 40, 93–111.
- Martin, A. D., Quinn, K. M., & Park, J. H. (2011). MCMCpack: Markov Chain Monte Carlo in R. Journal of Statistical Software, 42(9), 1–21. http://www.jstatsoft.org/v42/i09/.
- Mesoudi, A. (2008). An experimental simulation of the "copy-successful-individuals" cultural learning strategy: Adaptive landscapes, producer-scrounger dynamics, and informational access costs. *Evolution and Human Behavior*, 29, 350–363.
- Mesoudi, A. (2011). An experimental comparison of human social learning strategies: Payoff-biased social learning is adaptive but underused. *Evolution and Human Behavior*, 32, 334–342.
- Morgan, T. J. H., Rendell, L. E., Ehn, M., Hoppitt, W., & Laland, K. N. (2012). The evolutionary basis of human social learning. *Proceedings of the Royal Society B-Biological Sciences*, 279, 653–662.
- Ohmagari, K., & Berkes, F. (1997). Transmission of indigenous knowledge and bush skills among the Western James Bay Cree women of subarctic Canada. *Human Ecology*, 25, 197–222.
- Roes, F. L., & Raymond, M. (2003). Belief in moralizing gods. Evolution and Human Behavior, 24, 126–135.
- Rogers, A. R. (1988). Does biology constrain culture?,90, 819–831. American Anthropologist.
- Stout, D. (2002). Skill and cognition in stone tool production an ethnographic case study from Irian Jaya. Current Anthropology, 43, 693–722.
- Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364, 2405–2415.
- Trivers, R. (2000). The elements of a scientific theory of self-deception. Annals of the New York Academy of Sciences, 907, 114–131.
- West, S. A., Gardner, A., Shuker, D. M., Reynolds, T., Burton-Chellow, M., Sykes, E. M., et al. (2006). Cooperation and the scale of competition in humans. *Current Biology*, 16, 1103–1106.
- Whittingham, M. J., Stephens, P. A., Bradbury, R. B., & Freckleton, R. P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, 75, 1182–1189.