Full Model Description
premo_2020.nlogo
Version 1.0

This model description follows the guidelines of the ODD protocol (Grimm et al. 2010). The model used to collect the data presented in Premo (2020) runs on NetLogo 6.0.2. The code may need to be modified to run on later versions of NetLogo.

Purpose
This version of the accumulated copying error (ACE) model is designed to address the following research question: how does finite population size (*N*) affect the coefficient of variation (CV) of a continuous cultural trait under the assumptions that the only source of copying error is visual perception error and that the continuous trait can take any positive value (i.e., it has no upper bound)? The model allows one to address this question while assuming the continuous trait is transmitted via vertical transmission, unbiased transmission, prestige biased transmission, mean conformist transmission, or median conformist transmission. By varying the parameter, *p*, one can also investigate the effect of a mix of vertical and oblique transmission, whereby on average (1-*p*)*N* individuals learn via vertical transmission and *pN* individuals learn via either unbiased transmission, prestige biased transmission, mean conformist transmission, or median conformist transmission.

Entities, state variables, and scales
The "turtles" of NetLogo are used to represent individuals capable of transmitting cultural information from members of the "experienced generation" to members of the "naïve generation." The term generation is used loosely here. It does not refer to a human generation, but rather to the time required to transmit cultural information to all of the naïve individuals in a constant-sized population. In this case, the information transmitted is a continuously varying trait or attribute, like length or width, of a hand-made tool. This model is not spatially explicit, so the x, y coordinate of each agent is meaningless.

Global Variables
seed
* Specifies the value of random-seed. Each unique simulation run gets its own unique seed value. The seed values used in Premo (2020) are provided in the experiments available in BehaviorSpace.

N
* Finite population size. The model assumes population size remains constant and that all individuals engage in cultural transmission each generation.

w
* Weber Fraction for visual perception error. This provides a hard ceiling and floor on the proportional size of copying error attributed to the limits of our visual perception. More specifically, the absolute value of the size of the error attributed to the limits of our perception cannot be greater than (Xt-1 * *w*).

p
* Probability of engaging in non-vertical cultural transmission. On average *pN* naïve individuals learn via the non-vertical transmission mechanism defined by *c*.

c
* Non-vertical cultural transmission. This variable is used to distinguish whether individuals will learn via unbiased, prestige biased, mean conformist, or median conformist biased in place of vertical cultural transmission when $p>0$. Note that each simulation run can include just one of these non-vertical transmission mechanisms.

starting-X
* The Xt-1 and Xt of every individual are initialized with this value at the start of the simulation run.

count-errors-too-big
* This is a counter that keeps a running tally of how many times copy error exceeds the acceptable error size as defined by the Weber Fraction for visual perception error. It should never exceed 0 during the course of a simulation. If the value of this variable ever does exceed 0, then there is a bug. This was used to test the code and demonstrate that none of the simulations included "perceptible" error.

max-CV
* The maximum value of CV(Xt) recorded during each simulation run. This is reported as *max* CV($X_{N,t}$) in the paper.

mean-Xt-1
* The mean of the Xt-1 displayed in the "experienced" generation. This is the value that naïve agents will attempt to copy when they engage in mean conformist biased transmission. This variable is updated at the start of every time step.

median-Xt-1
* The median of the Xt-1 value displayed in the "experienced" (t-1) generation. This is the value that naïve agents will attempt to copy when they engage in median conformist biased transmission. This variable is updated at the start of every time step.

prestige-Xt-1
* The Xt-1 value displayed by the most prestigious member of the "experienced" generation. This is the value that naïve agents will attempt to copy when they engage in prestige biased transmission. This variable is updated at the start of every time step.

median-one
* The agent who displays median-Xt-1. This individual will serve as the teacher/model for all of the naïve individuals who learn via median conformist biased cultural transmission during the current time step.

prestigious-one
* The most prestigious member of the "experienced" generation. Prestigious-one is chosen randomly at the start of each time step. That is to say, prestige is defined arbitrarily and prestige is not inherited. This individual will serve as the teacher/model for all of the naïve individuals who learn via prestige biased cultural transmission during the current time step.

sum-Vk
* The sum of V_k over all ticks. As described in Premo (2020), V_k is variance in number of naïve individuals taught per time step. At the end of each simulation run, sum-Vk is divided by the number of ticks to provide mean-Vk.

mean-Vk
* The mean of V_k over all ticks. This is reported as V_k in the paper.

ticks-plot
* This is displayed on the interface to identify when the plots were last updated.

Other global variables used for data collection/analysis (described further with comments in the source code): mean-Xt-pop-0 through mean-Xt-pop-500000; var-Xt-pop-0 through var-Xt-pop-500000; CV-Xt-pop-0 through CV-Xt-pop-500000; mean-lnXt-pop-0 through mean-lnXt-pop-500000; var-lnXt-pop-0 through var-lnXt-pop-500000

Turtle Variables
Xt
* The value of the continuous trait *X* displayed by ego at time *t*. This represents the continuous trait ego displays following cultural transmission from the experienced generation. Xt includes the effect of proportional copy error. Xt is set to 0 at the start of each time step. Xt-1 will be set to Xt at the end of each time step.

Xt-1
* The value of the continuous trait X displayed by ego at time *t*-1. *t*-1 refers to the "experienced" generation (one generation prior to the current generation, *t*).

number-students
* the number of "naïve" individuals ego taught during the course of the current time step. This is used to calculate V_k, which is then added to sum-Vk, during each time step. number-students is set to 0 at the start of each tick.

xcor, ycor
* The x, y coordinate of each agent marks its location in 2-dimensional space. This is NOT a spatially explicit model, so these variables are not used at all in the code.

size and color
* Both size and color are used only for visualization in the interface and thus they are purely cosmetic.

Process overview and scheduling

The *go* method provides the schedule of procedures called during each time step. The "ask" primitive ensures that agent order is randomized during each procedure. The *go* method has three main components: it (1) operationalizes the cultural transmission of a continuous trait X from the "experienced" generation (Xt-1) to the "naïve" generation (Xt), (2) manages data collection during each simulation run, and (3) provides a "stop condition" for automatically stopping each simulation run.

Cultural transmission

The beginning of each time step involves updating global variables that will be used later in the *go* method if $p>0$. When $p>0$ some agents will learn from either the most prestigious individual, the individual with the median value (when N is even, "ties" are broken randomly), or the mean of Xt-1 displayed by all turtles, depending on c. A turtle is chosen randomly to serve as prestigious-one and then prestige-Xt-1 is set to prestigious-one's Xt-1 value. mean-Xt-1 is set to the mean Xt-1 of all turtles. Setting median-one and median-Xt-1 is a bit more involved when there is an even number of individuals due to the way in which "median" works in Netlogo. For a list with an even number of items, the NetLogo primitive, median, returns the average of the two items in the middle of the ordered list. This is unacceptable for our current needs because we want naïve individuals to learn from an individual rather than a mean of two values. So, the code in this section customizes the way in which median-one and median-Xt-1 are set when N is an even number. Instead of taking the average of the two items in the middle of the ordered list, one of the two middle items are chosen randomly to serve as median-Xt-1 and then median-one is set to the turtle that displays Xt-1 equal to median-Xt-1.

Next, every turtle sets its number-students equal to 0. It is important that this occurs before cultural transmission so that sum-Vk (which is used to calculate mean-Vk, which in turn is used to calculate the effective population size of X at the end of each run) provides the sum of V_k values calculated for each individual time step.

Then comes the actual transmission of cultural information. Each agent learns via vertical transmission with probability $1-p$ or the non-vertical transmission mechanism defined by c with probability p. Note that if $p=0$, then all transmission occurs via vertical cultural transmission (*learn-vertical*). However, if $p>0$, then agents can learn via either prestige biased (learn-prestige), unbiased (*learn-unbiased*), mean conformist (*learn-mean-conformist*), or median conformist biased (*learn-median-conformist*) transmission instead of vertical transmission (*learn-vertical*). These submodels are described in more detail below.

After cultural transmission from the experienced to the naïve generation, but before the end of the time step, every turtle sets its Xt-1 equal to its Xt. This overwrites the experienced generation's X values with the values acquired by naïve individuals during the current time step. This is necessary because it makes the trait values acquired by the naïve generation during the current time step available for transmission from the experienced generation during the subsequent time step when a new generation of naïve individuals will be learning from the present one. In other words, this code operationalizes the "ageing" of the naïve generation of today into the experienced generation of tomorrow, so to speak. Note that I use "generation" loosely here; it does not refer to the actual generation time of humans.

Data collection
The next section of the *go* method provides code related to data collection. If the coefficient of variation of Xt is greater than max-CV, then max-CV is set to the coefficient of variation of Xt. sum-Vk is set to sum-Vk plus the variance of number-students among all turtles (V_k). Plots are updated every 5000 ticks. Data on the mean, variance, and CV of Xt are collected every 10,000 ticks and stored in time-stamped global variables that are saved to output files by BehaviorSpace.

Stop condition
The final section of the *go* procedure provides the stop condition. The experimental design employed in Premo (2020) requires that *go* is repeated 500,000 times in each simulation run. After the 500,000th tick, mean-Vk is calculated before the simulation is terminated. When running an experiment from BehaviorSpace, data collected throughout each run are sent to a .csv file at the end of each simulation. Each BehaviorSpace experiment will result in at least one .csv file (the user can choose to save the data in up to two different formats) containing the data collected from every simulation run in that experiment.

Design concepts
There are two *basic principles* addressed in this model. The first concerns how different mechanisms of cultural transmission affect the effective population size (N_e) of a cultural trait. Holding N constant, increasing oblique transmission at the expense of vertical transmission decreases the effective population size of a trait. The second basic principle is that finite population size introduces a systematic bias to estimating the expected value of the random variable X under proportional error when the distribution of the random variable being sampled by N transmission chains is right-skewed, as is the case under pure vertical cultural transmission.

As one might suspect of any model of cultural transmission, agent *interaction* is a key component. Agent interaction is mitigated by the type and frequency of different mechanisms of cultural transmission. The nature of the *interaction* of agents between transmission chains is reflected in the effective population size of the culturally transmitted trait. When agent interaction is constrained to vertical transmission, whereby an agent learns from the previous member of its own transmission chain rather than from a member of a different chain, the effective population size of the cultural trait X is infinitely large. Increasing the likelihood of unbiased, prestige biased, or conformist biased transmission, whereby agents learn from members of other transmission chains reduces the effective population size of the cultural trait.

Agents' *sensing* abilities vary with p and c. When p=0, each agent can only sense its own Xt-1 value. When p>0, each agent has probability p of sensing an Xt-1 value from outside its own transmission chain—this might be the median Xt-1, the mean Xt-1, or an Xt-1 chosen at random under prestige biased or unbiased cultural transmission.

The model is initiated with a user-defined seed, which affects the *stochastic* processes in the model. A few of the model's most important components involve stochastic processes. Perhaps the most obvious stochastic process is the one involved in determining the size of the error added to the target value during each transmission event. As described in more detail below, error-size is the product of the target value (e.g., Xt-1) and a random number pulled from a uniform distribution bound by w, which represents the Weber Fraction for visual perception. The

resulting error-size is either added to or subtracted from the target value (each possibility occurs with equal probability). Another important stochastic process can be found in the ways by which prestige-Xt-1 and teacher-Xt-1 are set. In both cases, the value is chosen at random from the population of turtles. It is also worth noting that the code for setting median-Xt-1 also involves stochasticity when *N* is an even number.

Some of the *observations* in this model are associated with describing the effective population size of the continuous trait X under different mixes of vertical and non-vertical cultural transmission. In particular, sum-Vk is used to calculate mean-Vk, which provides the denominator of the equation used to calculate the effective population size of trait X from so-called "demographic" data on the variance in the number of naïve individuals taught per member of the experienced generation. Other *observations* allow one to track how the mean, variance, and CV of X change through time in the population of *N* transmission chains. Although these values (e.g., mean-Xt-pop-10000) were collected every 10,000 time steps, only the final value collected after time step 500,000 in each simulation run was used in the analyses presented in Premo (2020). Finally, some *observations* were made to verify the code: e.g., count-errors-too-big.

Initialization

Table 1 provides the parameter values used to initialize the simulations reported in Premo (2020). These values can be found in the published paper as well as in the experiments saved in BehaviorSpace. After the random-seed is set to seed, the global variables max-CV, count-errors-too-big, sum-Vk, and mean-Vk are all set to 0. Then *N* turtles are created, and each agent's Xt and Xt-1 are both set to starting-X. Note that agent size, color, heading, xcor, and ycor have no significance in this model.

Table 1. Parameter values used to initialize the simulations reported in Premo (2020).

Parameter	**Value(s)**
Weber Fraction, *w*	.03
starting-X	10
Population size, *N*	10, 25, 50
Prob. non-vertical, *p*	0, 1.0e-6, 1.0e-5, 1.0e-4, 1.0e-3, .01, .05, .10, .25, .50, 1
Cultural transmission, *c*	unbiased, prestige, mean-conformist, median-conformist
seed	1-30

Replication

To generate the data presented in Figures 5-7 in Premo (2020), run the experiments listed in BehaviorSpace, which can be accessed from the Tools drop-down menu. The main experiment, named "vertical_and_c_CT", takes care of all values of *p* greater than 0. Of those 3600 runs, there were 3 runs that—due to chance—did not include a non-vertical transmission event when *N*=10 and *p*=1.0e-6. To ensure that each run includes at least one non-vertical cultural transmission event when *p*>0, I replaced those 3 runs in which there was not at least one instance of non-vertical cultural transmission with data collected from "vertical_and_prestige_2_more_seeds" (seed=31, 32 replace seed=18, 29) and "vertical_and_unbiased_1_more_seed" (seed=31 replaces seed=18). "vertical_CT_only" deals with the 90 simulations in which *p*=0. The final dataset contains a total of 3690 simulation runs.

Input Data
The model does not require any input data or additional files to initialize a simulation run.

Submodels
learn-vertical
This submodel operationalizes vertical cultural transmission while incorporating proportional copying error. With vertical cultural transmission, every naive individual attempts to copy the attribute value it displayed in the previous time step, or the "experienced generation." In other words, vertical transmission occurs by transmitting Xt-1 to Xt (plus proportional copying error) *within* each turtle.

First, the local variable "error-size" is set to the product of Xt-1 and a random number drawn from a uniform distribution between 0 and *w*. Note that error-size will be different for each transmission event even though *w* is the same for all turtles. Next, if error-size is greater than (Xt-1 * *w*), which should never be the case, then count-errors-too-big is incremented by 1 and a custom error message is sent to the observer window at the bottom of the "interface." Then the turtle sets its Xt to either (Xt-1 + error-size) or (Xt-1 - error-size) with equal probability. That is to say, there is an equal probability that the error increases or decreases Xt-1 by the amount given by error-size. At this point, the naïve individual has learned from its "parent" and proportional perception error has affected the value ultimately displayed by the naïve individual. Finally, the turtle increments number-students by 1 to reflect the fact that it learned from the previous generation of its own transmission chain.

It may seem confusing at first that vertical cultural transmission from the experienced generation to the naïve generation occurs *within* each turtle rather than between two turtles. But by representing different generations with two different turtle state variables—Xt-1 and Xt—rather than with two different collectives of turtle agents, I was able to avoid creating and destroying *N* turtles each time step. Although this choice does not affect the model dynamics in any way, it means that the program runs much faster than if I had represented the creation of a new generation with actual births of agents every time step.

learn-unbiased
This submodel operationalizes unbiased cultural transmission while incorporating proportional copying error. With unbiased cultural transmission, every naive individual attempts to copy the Xt-1 displayed by an individual chosen randomly (and with replacement). Although every member of the experienced generation is equally likely to be chosen by each member of the naïve generation, some of the former will transmit their attribute to more than one member of the naive generation while other experienced individuals will not transmit their attribute at all. The resulting variance in the number of "progeny" among members of the experienced generation is due to the well-known effects of randomly sampling a finite population.

First, ego picks a teacher at random from all turtles (including itself). The local variable "teacher" is set to that randomly chosen individual. Serving as a teacher for one naïve individual does not exclude one from serving as a teacher for other naïve individuals. Second, the local variable "teacher-Xt-1" is set to the Xt-1 value of teacher. Third, the local variable "error-size" is set to the product of teacher-Xt-1 and a random number drawn from a uniform distribution

between 0 and *w*. Note that error-size will be different for each transmission event even though *w* is the same for all turtles. Next, if error-size is greater than (teacher-Xt-1 * *w*), which should never be the case, then count-errors-too-big is incremented by 1 and a custom error message is sent to the observer window at the bottom of the interface. Then the turtle sets its Xt to either (teacher-Xt-1 + error-size) or (teacher-Xt-1 - error-size) with equal probability. That is, there is an equal probability that the error increases or decreases teacher-Xt-1 by the amount given by error-size. At this point, the naïve individual has learned from teacher, an individual it chose at random, and proportional perception error has affected the value ultimately displayed by the naïve individual. Finally, teacher is asked to increment number-students by 1 to reflect the fact that it taught another member of the naïve generation.

learn-prestige
This submodel operationalizes the transmission of prestige-Xt-1 to the naïve generation while incorporating proportional copying error. Under prestige biased cultural transmission, members of the naive generation attempt to copy the attribute of the individual deemed to be the most prestigious member of the experienced generation. Following the method employed by Eerkens and Lipo (2005), the "prestigious-one" is chosen randomly from all turtles at the start of each time step (see above).

First, the local variable "error-size" is set to the product of prestige-Xt-1 and a random number drawn from a uniform distribution between 0 and *w*. Note that error-size will be different for each transmission event even though *w* is the same for all turtles. Next, if error-size is greater than (prestige-Xt-1 * *w*), which should never be the case, then count-errors-too-big is incremented by 1 and a custom error message is sent to the observer window at the bottom of the interface. Then the turtle sets its Xt to either (prestige-Xt-1 + error-size) or (prestige-Xt-1 - error-size) with equal probability. There is an equal probability that the error increases or decreases prestige-Xt-1 by the amount given by error-size. At this point, the naïve individual has learned from the most prestigious individual of the experienced generation and proportional perception error has affected the value ultimately displayed by the naïve individual after transmission. Finally, prestigious-one is asked to increment number-students by 1 to reflect the fact that it taught another member of the naïve generation.

learn-mean-conformist
This submodel operationalizes the transmission of mean-Xt-1 to the naïve generation while incorporating proportional copying error. Under what I call "mean conformist biased" transmission, members of the naïve generation attempt to copy the mean of Xt-1, just as in Eerkens and Lipo (2005). Following the method employed in the *go* method described above, the global variable mean-Xt-1 is set to the mean of Xt-1 at the start of each tick.

First, the local variable "error-size" is set to the product of mean-Xt-1 and a random number drawn from a uniform distribution between 0 and *w*. Note that error-size will be different for each transmission event even though *w* is the same for all turtles. Next, if error-size is greater than (mean-Xt-1 * *w*), which should never be the case, then count-errors-too-big is incremented by 1 and a custom error message is sent to the observer window at the bottom of the interface. Then the turtle sets its Xt to either (mean-Xt-1 + error-size) or (mean-Xt-1 - error-size) with equal probability. There is an equal probability that copying error increases or decreases mean-

Xt-1 by the amount given by error-size. At this point, the naïve individual has attempted to copy the mean value of Xt-1 in the experienced generation and proportional perception error has affected the value ultimately displayed by the naïve individual after transmission. Note that in this case there is no "mean-one" to ask to increment its number-students simply because no turtle will have an Xt-1 that is equal to mean-Xt-1. Because the trait passed on to naïve individuals is a composite of all of the members of the experienced generation, mean-Vk is not interpretable under mean conformist biased transmission. Given this limitation, I use the effective population size generated by median conformist biased transmission for both types of conformist biased transmission. To the extent that this introduces a bias in the results that address the relationship between the effective population size of X and equilibrium variation in X under mean conformist biased transmission, it would *overestimate* the effective population size of X under mean conformist transmission. This is due to the fact that there is a small amount of vertical cultural transmission in median conformist transmission that is not present in mean conformist transmission. This small amount of vertical transmission increases the effective population size of X under median conformist biased transmission in a way that would not be possible under mean conformist biased transmission where no single individual ever serves as a teacher.

learn-median-conformist
This submodel operationalizes the transmission of median-Xt-1 to the naïve generation while incorporating proportional copying error. Under what I call "median conformist biased" transmission, members of the naïve generation attempt to copy the median value of Xt-1. Following the method employed in the *go* method described above, the global variable median-Xt-1 is set to the median value of the experienced generation at the start of each tick.

First, the local variable "error-size" is set to the product of median-Xt-1 and a random number drawn from a uniform distribution between 0 and *w*. Note that error-size will be different for each transmission event even though *w* is the same for all turtles. Next, if error-size is greater than (median-Xt-1 * *w*), which should never be the case, then count-errors-too-big is incremented by 1 and a custom error message is sent to the observer window at the bottom of the interface. Then the turtle sets its Xt to either (median-Xt-1 + error-size) or (median-Xt-1 - error-size) with equal probability. That is to say, there is an equal probability that copying error increases or decreases median-Xt-1 by the amount given by error-size. At this point, the naïve individual has learned from the individual who displays the median value of Xt-1 and proportional perception error has affected the value ultimately displayed by the naïve individual after transmission. Finally, median-one is asked to increment number-students by 1 to reflect the fact that it taught another member of the naïve generation.

References

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Contact Information

This model was programmed by Luke Premo (Department of Anthropology, Washington State University and the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology). One of the best things about computer simulation programs is that they can often be improved with the help of other researchers. The more sets of eyes that pass over the code, the better. So, please, have a look at the commented source code under the "code" tab. Any comments, questions, or corrections are always welcome. Feel free to contact me at:

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