

The evolution of culture: From primate social learning to human culture

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Cultural transmission in our species works most of the time as a cumulative inheritance system allowing members of a group to incorporate behavioral features not only with a positive biological value but sometimes also with a neutral, or even negative, biological value. Most of models of dual inheritance theory and gene-culture coevolution suggest that an increase, either qualitative or quantitative, in the efficiency of imitation is the key factor to explain the transformation of primate social learning in a cumulative cultural system of inheritance as it happens during hominization. We contend that more efficient imitation is necessary but not enough for this transformation to occur and that the key factor enabling such a transformation is that some hominids developed the capacity to approve or disapprove their offspring's learned behavior. This capacity to approve or disapprove offspring's behavior makes learning both less costly and more accurate, and it transformed the hominid culture into a system of cumulative cultural inheritance similar to that of humans, although the system was still prelinguistic in nature.

imitation | teaching | assessor | dual inheritance | cultural transmission

Culture defined as variation acquired and maintained by indirect (basically stimulus and local enhancement) and direct (basically imitation) social learning is common in nature, but it reached an important level in *Homo sapiens* only when it led to a cultural evolution process with a great adaptive value (1, 2). Cultural transmission in our species works most of the time as a cumulative inheritance system allowing members of a group to incorporate behavioral features not only with a positive biological value, but sometimes also with a neutral, or even negative, biological value. It is not clear how cultural transmission has improved human adaptability, especially when other primates with well developed social learning abilities show comparably restricted ranges. Hence, we are left to answer the questions: what types of changes occurred during the hominization process that transformed typical social learning in primates into a cumulative cultural inheritance system similar to that of humans and what was the adaptive advantage that made these changes possible? The recent developments of the two closely related fields of gene-culture coevolution and dual inheritance theory provided, until now, the most convincing answers to these questions (for reviews, see refs. 3 and 4).

Boyd and Richerson (1) and Cavalli-Sforza and Feldman (5) had argued that social learning improves human adaptability by exempting individuals from the costs of individual learning (basically trial and error learning). Time costs and potential mistakes can make individual learning quite expensive, and therefore, if others individuals have already paid those costs, learning from the behavior of these individuals may be cheaper. Imitation allows individuals to acquire a vast store of useful knowledge without incurring the costs of discovering and testing this knowledge themselves.

Rogers (6), using a simple mathematical model, has shown that the fact that social learning (basically imitation) allows an individual organism to avoid the costs of learning does not increase the ability of that species of organism to adapt and is

insufficient to explain the adaptive success of human culture. He proved that, as long as the only benefit of imitation is that imitators avoid the cost of individual learning, imitation has no effect at all on the evolving organism's average fitness in the long run. Although imitators do very well when they are rare and individual learners are common, they do poorly when they are common and individual learners are rare. This means that at equilibrium the mean fitness of the population as a whole is the same as that in a population of purely individual learners.

Boyd and Richerson (7) have shown that Roger's result is robust. However, they also show that imitation can be adaptive and increase average fitness of imitators if it makes individual learning less costly or more accurate. The first condition (i.e., imitation makes individual learning less costly) is satisfied if individuals use individual learning when it is cheap and reliable and switch to imitation when individual learning is expensive. The second condition (i.e., imitation makes individual learning more accurate) is satisfied if imitation allows the accumulation of behaviors (i.e., the direct and accurate copying of behaviors) that no individual learner could acquire by himself from one generation to the next. That is, it allows cumulative cultural evolution.

For Boyd and Richerson (7), cumulative cultural evolution is not present in chimpanzees culture because chimpanzees unfold their imitative learning abilities in a less consistent manner than humans do. The authors show that, although cultural accumulation is adaptive, the evolution of the psychological capacities that make it possible is difficult when these capacities are rare. Boyd and Richerson also suggest that it is likely that the cognitive capacities that allow the initial evolution of an efficient capacity of imitation must evolve as a side effect of some other adaptive change, e.g., a capacity for theory of mind that may have initially evolved to allow individuals to better predict the behavior of other members of their social group. Tomasello (8) claims that the key for the transformation of social learning in hominids into a human cultural inheritance system was a qualitative change in imitation ability, which requires as a previous step that individuals develop a capacity for a theory of mind that would enable them to perceive their peers as intentional beings with a similar mind.

In this paper, we suggest that, in contrast to the common assumptions in models of gene-culture coevolution and dual inheritance theory, imitation in human and nonhuman primates is basically a tool that allows an individual to learn the behaviors that other individuals of the population exhibit but to refrain from adopting the behaviors until after further evaluation. From this definition of imitation as a process of observational learning but not of replication of behaviors without evaluation, we contend that an increase, either qualitative or quantitative, in the efficiency of imitation is not enough to explain the transformation of primate social learning into a cumulative cultural system

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of inheritance in the strict sense. The key factor enabling such a transformation was the fact that some hominids developed the capacity to approve or disapprove their offspring's learned behavior. It was this capacity to approve or disapprove offspring's behavior that makes learning both less costly and more accurate and that transformed the hominid culture into a system of cumulative cultural inheritance similar to that of humans, although the system was still prelinguistic in nature.

The Evolution of Culture

Imitation Is Necessary for Human Cultural Transmission but It Is Not Enough. We consider that the adoption of a learned behavior in primates can be defined as a process with three steps: (i) to discover and to learn a behavior, (ii) to test and to evaluate the learned behavior, and (iii) to reject or to incorporate the behavior into the behavioral repertoire (see ref. 9 for a more detailed explanation). Primates can discover and learn a behavior (the first step) through trial-and-error learning, insight, local enhancement, imitation, etc., but afterward individuals must test and evaluate learned behavior through their evaluative brain structures, and they can choose to adopt or reject the behavior that they have learned. Primates maintain intact the evaluation systems required for the trial-and-error learning, and these systems are phylogenetically older, in mammals, than the capacity of imitation.

We suggest that individual learning (basically trial-and-error learning) and social learning (basically local and stimulus enhancement and maybe imitation) in primates represent two alternative mechanisms for discovering a given behavior that do not compromise the final adoption of the behavior. Therefore, nonhuman primate imitators learn the behaviors they observe but evaluate the behaviors before deciding which behavior is going to be incorporated into their behavioral repertoire. Besides, they can rectify the previously adopted decision if the reward obtained from the behavior changes. Heyes (10) claims that available evidence suggests that behaviors acquired through imitation are no more likely than those acquired through any other form of learning to be retained if they are punished, if alternative behaviors are rewarded equally, or if alternative behaviors are preferentially rewarded. Galef (11) suggests an approach to analysis of social learning processes that assumes that social interactions affect the probability of introduction of novel behavior patterns into a naïve individual's repertoire and that consequences of engaging in a socially learned behavior determine whether that behavior continues to be expressed. However, even if it were possible to omit the evaluation of behavior, it would be dangerous to do it because the imitation capacity is far from being perfect, and therefore, the individuals generate by mistake behaviors different from those of the cultural models. Furthermore, it is well known that, even when the behavior is correctly copied, human and nonhuman primates can modify it to adjust it to the actual and successive environments in a process that Boyd and Richerson (1) have called guided variation.

According to this reasoning, we claim that imitation in the hominid lineage did not evolve as an alternative to rigorous assessment of individually learned behavior, i.e., a mechanism to adopt conducts without evaluating them. Imitators learn easily the diverse cultural variants present in the population, but imitation does not act as an inheritance system that allows the reproduction of the phenotypic structure of the parental population. We think that imitation arises and acquires adaptive meaning as an instrument that facilitates the learning of those adaptive behaviors that are difficult to develop through individual learning or through indirect social learning, e.g., local and stimulus enhancement. The reason is that imitation, unlike indirect social learning mechanisms, allows an individual to copy the behavior of another individual without having

to reinvent it. Accordingly, the greater the adaptive significance and the difficulty to develop a given behavior through individual learning, the greater the selection pressure should be in favor of the development of imitation processes, ensuring its rapid acquisition.

Reader and Laland (12) found empirical evidence that innovation and social learning frequencies covary across species, a fact that is in conflict with the view that there is an evolutionary tradeoff between reliance on individual learning and imitation as the current models of gene-culture coevolution suggest (see, for example, ref. 3). These findings provide an empirical link between behavioral innovation, imitative cognitive capacities, and brain size in mammals. Thus, they imply that the social and ecological intelligence hypotheses for brain evolution must not necessarily be regarded as alternatives and that multiple sources of selection favored the evolution of a large primate executive brain. Henrich and McElreath (4) suggest that evolution of both individual and social learning (including imitative capacities) has been consequence of an intertwined adaptive response to increasing amounts of environmental variability. We agreed with this proposition, and we maintain that the coevolution of individual learning and imitation responds to the following process: an increase of environmental variability favors individual learning, and this favors, in turn, the development of social learning abilities through the exploitation of a body of adaptive knowledge that is stored in the individually learned behavioral repertoire of the population. This development is adaptive whenever the environment does not change so quickly that it cancels the biological value of what was learned by the previous generation. In this situation of moderate environmental variability, imitation can be more favored by natural selection than other forms of indirect social learning (although it requires a greater cognitive investment) alone, but only if it increases the probability that imitators discover and profit from adaptive behaviors that can be learned only by very few individuals through individual or indirect social learning. However, it should be noted that the development of imitative abilities does not necessarily generate in turn a positive feedback process in favor of higher levels of innovation and insight. Those individuals who imitate get access to those behavioral innovations from the individuals with a higher intellectual capacity, not necessarily their parents, and therefore, imitation may restrain the adaptive advantage of a greater investment on intellectual capacity. In other words, the development of imitation does not necessarily lead to a gradual development of innovative capacity as it happened in our species.

The Capacity to Approve or Disapprove of Offspring's Learned Behavior. We suggest that the transformation of primitive hominid social learning, which was probably rather similar to that of today's chimpanzees (i.e., based on indirect social learning mechanisms and rudimentary imitative abilities), into a human cultural transmission system required that our hominid ancestors developed the capacity to approve or disapprove of offspring's learned behavior. Our thesis holds that the simultaneous presence of both capacities in our hominid ancestors, imitation and approval/disapproval of offspring's learned behavior, represented a radical change in the rudimentary cultural transmission of first hominids. Individuals with both abilities, which we call assessors, generated a cultural inheritance system in a strict sense, because by approval/disapproval, they constrained the behavior that offspring incorporated into their repertoires (9).

Furthermore, assessor parents facilitate the evaluation of children's learned behavior, making learning both less costly and more accurate. Approval or disapproval of offspring's behavior works as a new evaluative criterion, which is particularly useful when evaluation is difficult and has little reliability. Approval favors the implementation of behavior, which has no immediate positive evaluation for the individual experiencing it. Disap-

proval allows the offspring to acquire information about behaviors they are self-discovering without having to experience all their negative consequences. This allows offspring to take advantage of parental expertise and avoid learning costs. Assessor parents make available to the offspring all they had learned either referent to the things they can do or to the things they cannot do. The former can be imitated from individuals that are not the parents, but the latter is transmissible only between parents and offspring by disapproval of behavior. In this way, assessor cultural transmission favors instead of restrains an increase investment in the intellectual capacity.

Assessor cultural transmission transforms culture into an inheritance system in a rigorous sense, increasing phenotypic resemblance among parents and offspring for those behaviors that parents know and have previously categorized. Individual learning represents an answer to rapid environmental changes that natural selection cannot face, whereas assessor cultural transmission implies an attempt to take advantage of what has been learned in an individual manner when its validity holds for long enough, but not long enough for genetic adaptation to emerge, e.g., dozens or even hundreds of generations. This is likely the rhythm of environmental change that has characterized the hominid evolution (4). Besides approval and disapproval of offspring's learned behavior increases the reliability of imitation generating a cumulative cultural inheritance system that is capable of keeping and cumulating the behavioral findings of a generation and passing it on to the next. The need for fidelity in the copied behavior for cultural transmission to work as a cumulative inheritance system is a serious handicap to explain cultural transmission in humans, as it is noted by several researchers (see, for example, ref. 13). In our hypothesis, disapproval of badly imitated behavior forces the imitator to repeat the process, and this repetition makes the increase in fidelity in the copied behavior possible, hence allowing cumulative cultural transmission. Moreover, an assessor cultural inheritance system is flexible despite its reliability because it does not impede dissemination of behavioral innovations, which lack previous evaluation.

Cultural Dynamic. A simple model of cultural transmission that can be applied to assessor hominids ancestors can illuminate previous ideas better. Let us define the probability that an individual without capacity of imitation acquires behavior i as $h_i\beta_i$, where h_i is the probability that an individual discovers the behavior i , and β_i is the probability that the behavior will be included in his repertoire. If the individual already knows an alternative (behavior j) to behavior i , the probability that behavior i will be included in his repertoire will be equal to $h_i\beta_{ij}$, where β_{ij} is the probability that he chooses i instead of alternative behavior j . However, if the individual also has the imitation capacity and there are cultural models in the population, the probability of his including i in his repertoire will be $h_i^*\beta_{ij}$, where h_i^* is the probability that an individual learns either by individual learning or by imitation behavior i , and equals $h_i^* = h_i + (1 - h_i)\alpha$, where α represents the efficacy of the process of imitation, and $(1 - h_i)\alpha$ measures the net effect of this process. Therefore, an increase in the imitation capacity is expressed as an increase in the value of α .

During ontogeny, individuals learn by imitating the behaviors that their parents (vertical transmission) and others individuals of the population (oblique and horizontal transmission) exhibit. We assume that imitation capacity is well developed in the individual ($a \approx 1$) and that population size is small enough so that he can observe all of the behavioral variants present in the population during his life cycle. This means that $h_i^* \approx 1$ for any behavior i present in the population. Under these circumstances, the incorporation of behavior i , assuming that there is only one other alternative (behavior j), will depend on β_{ij} . We assume that

Table 1. Assessor cultural transmission matrix

	Offspring	
	Behavior j	Behavior i
Behavior mother i	$\beta_{ij} + (1 - \beta_{ij})\delta$	$1 - \beta_{ij} - (1 - \beta_{ij})\delta$
Behavior mother j	$\beta_{ij} - \beta_{ij}\delta$	$1 - \beta_{ij} + \beta_{ij}\delta$

if $\beta_{ij} > 0.5$, the payoff of behavior i is greater than that of behavior j , and vice versa. If $\beta_{ij} = 0.5$, then there are no differences in terms of reward between behaviors i and j , or at least the individual's brain evaluative system cannot detect them.

We distinguish two types of individuals: imitators who can imitate very efficiently ($\alpha \approx 1$) and assessors who, in addition to being able to imitate ($\alpha \approx 1$), can also approve or disapprove of offspring's behavior. If individuals are only imitators but not assessors, the equilibrium frequencies of behaviors i and j will be (in absence of selection) β_{ij} and $\beta_{ji} = 1 - \beta_{ij}$, respectively. If individuals are assessors, the probability that an individual will include i into his repertoire will depend on his parents, and we suppose, for simplicity, that only the mother approves or disapproves of a child's behavior. In such conditions, the probability that an individual assessor will incorporate definitively into his behavioral repertoire one of these behaviors (i or j) at the end of his development is given by the transmission matrix in Table 1, where β_{ij} is, as defined before, the probability of accepting behavior i instead of j when the individual knows both behaviors. Parameter δ measures the efficacy of maternal approval or disapproval, whereas $(1 - \beta_{ij})\delta$ and $\beta_{ij}\delta$ measure the net effect of such approval or disapproval. If $1 \geq \delta > 0$, the individual is an assessor, and if $\delta = 0$, the individual is an imitator but not an assessor. Let us assume that the individuals of a population exhibit two alternative cultural behaviors i and j with frequencies p and $q = 1 - p$, respectively. If $\delta < 1$, it can be shown that, in absence of selection, the equilibrium phenotypic frequencies of behaviors i and j converge as before to β_{ij} and $1 - \beta_{ij}$, respectively, although slowly. However, if $\delta = 1$, the system maintains the initial frequencies irrespective of the value of β_{ij} and $1 - \beta_{ij}$ replicating the phenotypic structure of the parental generation (see *Appendix*).

Let us now assume that selection is introduced in such a way that the ratio of fitness of behaviors i and j is $1:1 - s$, and that genetically the capacity to approve or disapprove of offspring's learned behavior is controlled by an haploid genetic system with two alleles, A for the assessor and a for the nonassessor. Mutation is absent. Then, it is possible to show that the assessor genotype A ($\delta_A > 0$) can invade a population of imitator, nonassessor genotypes a ($\delta_a = 0$) and that it will also be stable against invasion by the nonassessor genotype (see *Appendix*). This means that if there are fitness differences between behaviors i and j , selection favors individuals with greater δ .

What is the difference between the model presented here and the basic standard model derived from gene-culture coevolution and dual inheritance theories? In the basic standard model of Boyd and Richerson (ref. 1, chapter 3), each individual of the new generation chooses a cultural model from the previous generation (either the parents or an individual taken at random) and adopts his behavior: i , with probability p , or j , with probability $q = 1 - p$. Afterward, he meets another individual and they compare their behaviors. If the behaviors coincide (with probability $p^2 + q^2$), they maintain the behaviors. If the behaviors are different (with probability $2pq$), each of the individuals can adopt one or the other with probability = 0.5, i.e., imitation without evaluation is unbiased. This could happen several times. The result is that the initial frequencies p and q of the two alternative cultural behaviors i and j are maintained ($p' = p^2 + pq = p$). Therefore, culture (imitation without evaluation)

replicates the phenotypic structure of the parental generation and behaves as a system of inheritance. From this unselective model, biased transmission models that favor the transmission of some variants above others can be built. For example, in the direct bias model of a qualitative character of Boyd and Richerson (1), naive individuals select with a bias B one of the variants. Although this bias is analogous to our β_{ij} , its effect in the direct bias model leads to a very different result [$p' = p^2 + pq(1 + B) = p + Bp(1 - p)$]. That is, directly biased transmission creates a force that always increases the frequency of the variant that is favored by the bias. Therefore, other forces being absent, the variant i tends to fixation instead of to β_{ij} as it occurs in our model with imitator nonassessors.

Besides, most of the standard models used to analyze the evolution of culture consider that an evolutionary tradeoff exists between individual learning and imitation (7, 14–16). All such models have consistently found that an environment that varies substantially in time and space will favor a greater dependence on individual experience, whereas a more constant environment favors imitation without evaluation, i.e., imitation as an unbiased inheritance system. In our model, imitators always test learned behavior until they make a decision about whether to accept it. Thus, if individuals are imitators but not assessors, culture is not a true inheritance system, and the initial frequencies p and q of behaviors i and j will change into β_{ij} and $\beta_{ji} = 1 - \beta_{ij}$, respectively. Only if individuals are assessors with δ values close to 1 will a true system of cultural inheritance develop. Therefore, an evolutionary tradeoff could exist, but it would be between assessor cultural transmission and individual learning. Now the conflict emerges if the parental generation transmits values that are not valid in the new environment in which the offspring is growing up. If the conflict arises, assessor individuals can overcome it modifying the learned value of a behavior, although such changes in the assessment of a cultural trait that is considered good are more difficult than would logically seem in the face of it (17), i.e., the assessor can modify the assessment only if the negative signals are intense enough. However, the tradeoff will not be frequent because the rate of environmental change that occurs during hominization is moderate (4).

The available evidence on primate social learning supports the proposed model. For example, culture in chimpanzees fit to a population of rudimentary imitators with small α and $\delta \approx 0$. We think that the anthropological and sociological evidence available in the human societies also adjust better to a model of cultural inheritance based on the approval or disapproval of offspring's behavior rather than to a model of replication/imitation. For example, approval and disapproval explain better the obstacles put up by cultural transmission to any modification involving the replacement of positively assessed behavior by a new type of behavior (17, 18). In any case it seems possible to test empirically which model better explains the properties of culture as a system of inheritance in both human and nonhuman primates.

Why Is the Assessor Rare?

Approval or disapproval of offspring's learned behavior has a cost for the assessor teacher just as many other traits of parental care have. The cost comes from the time and energy devoted to influence the offspring's behavior. The evolution of approval and disapproval of offspring's behavior will depend on whether the benefit of parental orientation outweighs the cost. However, we think that the fact that assessor cultural transmission has evolved only in the hominid line does not seem to be related to the importance of the implied costs, but rather with the need for complex cognitive development, similar at least to that possessed by chimpanzees within primates. According to some authors, imitation is present in some primates (19–21), but others doubt whether it really exists in primates living in their natural envi-

ronment (22, 23). However, there is a consensus among researchers that chimpanzees reared by human mothers/families are able to imitate. Probably a qualitative and quantitative improvement of imitative capacities required the development of a capacity for theory of mind (2, 8), which enables individuals to make a connection between the acts of other animals and their own acts and goal states.

The ability to approve or disapprove of offspring's learned behavior seems completely absent in primates (24–26). Probably the evolution of this capacity would require the previous development of the capacity to conceptually categorize learned behavior. The conceptual capacity to categorize is defined as the ability to categorize one's own and others' learned behavior in terms of values, i.e., positive or negative, or good or bad (27, 28). This definition implies the transformation of an unconscious and automatic mechanism for categorizing behavior used for individual learning into a conceptual categorization mechanism. The starting point of this conceptual ability to categorize depends on the evolution of certain functions. The first function is the development of the cortical system in such a way that, when conceptual functions appeared, they could be strongly linked to the limbic system. The second function is the development of a new kind of memory based on this linkage. This value–category memory system is able to categorize responses in the different brain systems that carry out perceptual categorization, and it does so according to the demands of the limbic brainstem value system. The third function is a special reentrant circuit that allows for continual reentrant signaling between the value–category memory and the ongoing global mappings that are concerned with perceptual categorization in real time. The final function is the development of some kind of symbolic memory connected to that memory system in charge of storing value categories and to those structures responsible for perceptual categorization. Probably, this would demand the development of neural circuits between regions in the cortex and from it to the thalamus. This memory for symbols and their related evaluative meanings would allow the conceptual coding of behavior in terms of positive or negative. Behavior rewarded during learning will receive, at least initially, a positive conceptual categorization, whereas behavior provoking some rejection will get a negative evaluation. We think that hominids with the ability to conceptually categorize learned behavior were able to approve or disapprove their offspring learned behavior.

Thus, according to our hypothesis, a chimpanzee may classify other individual's behavior as favorable or unfavorable with respect to himself and may act accordingly, but he is not able to attribute a protoconcept of good or bad to his own behavior, and this inability impedes the categorization of other individual's behavior as good or bad for that individual. Cheney and Seyfert (24) experimentally proved that macaque mothers are unable to transmit to their offspring information about the existence of hidden food or about the presence of a predator. Authors attributed this scarcely human behavior to the fact that monkeys are unable to distinguish between what they know and what others, including their offspring, know. We think it seems more reasonable to assume that mothers are not able to categorize their offspring's behavior as good or bad when taking the offspring's interests into account.

The capacity of approving or disapproving the children's learned behavior may be considered as an elementary form of teaching because individuals can transmit to their offspring the emotional value they gave to those behaviors they have previously learned and categorized. Really it is not a question of showing to the children how a thing can be done, but only if it must or must not be done and if it has been performed well or badly. Note that what is new is the increase in the ability to transmit a new kind of information, i.e., information about whether an individual must or must not continue testing a given

behavior as a function of what the parents know about it. Moreover, such transmission of values may start to work without the need for new mechanism of communication, given that disapproval of other individual's behavior is habitual in chimpanzees and other primates, but always with the purpose of modifying other's behavior when it directly affects the speaker. Notwithstanding, it seems that we humans have developed psychological mechanisms enabling assessor cultural transmission by making ourselves more receptive to parental directions. For example, Baum (29) states that humans are unusually sensitive to expressions of approval and disapproval by parents, whereas chimpanzee young brought up as human children remain quite wild and troublesome. Waddington (30) defines human beings as authority acceptors because children need to have the ability to be taught and they need to develop authority systems in their minds for that. Simon (31) suggested that humans possess a tendency to accept social influence that can be called human docility.

Finally, it is worth emphasizing that the hypothesis above about the evolution of culture could have interesting implications on the evolution of other typical traits of the human species. For example, we have proposed that conceptual classification of behavior in terms of positive/negative (good/bad) involves, according to its natural origin, a feeling of duty toward those positive behaviors, and this behavioral categorization and the feeling of "must" are the developmental roots of the ethical capacity (32). We have also shown that the adaptive advantage that implies the improvement of the assessor cultural transmission could be a key factor in the evolution of language (33).

Appendix

In the population there are two behaviors, i and j , and two genotypes, A and a , with different values of δ such that $1 > \delta_A > \delta_a > 0$. Therefore, there are four possible phenogenotypes, A_i , A_j , a_i , and a_j , with frequencies x_1, x_2, x_3 , and x_4 , respectively. The frequency of genotype A is $p = x_1 + x_2$, and the frequency of behavior i is $f = x_1 + x_3$.

The phenogenotypic frequencies in the next generation are calculated from the transmission matrix and are given by the following expressions.

$$\begin{aligned}x'_1 &= (\beta_{ij} + (1 - \beta_{ij})\delta_A)x_1 + (\beta_{ij}(1 - \delta_A))x_2 \\x'_2 &= ((1 - \beta_{ij})(1 - \delta_A))x_1 + (1 - \beta_{ij} + \beta_{ij}\delta_A)x_2 \\x'_3 &= (\beta_{ij} + (1 - \beta_{ij})\delta_a)x_3 + (\beta_{ij}(1 - \delta_a))x_4 \\x'_4 &= ((1 - \beta_{ij})(1 - \delta_a))x_3 + (1 - \beta_{ij} + \beta_{ij}\delta_a)x_4\end{aligned}$$

In absence of selection the equilibrium frequencies will be

$$\hat{p} = p$$

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$$\hat{f} = \beta_{ij}.$$

Therefore, for $1 > \delta_A > \delta_a > 0$, the allele frequency remains at its initial value p , but the phenotypic frequencies of behaviors i and j converge to β_{ij} and $1 - \beta_{ij}$, respectively, which are the values that would be attained in absence of assessor cultural transmission with only imitation, i.e., with $\delta_A = \delta_a = 0$. However, note that if all individuals are assessors with $\delta_A = \delta_a = 1$, the initial phenotypic frequencies will not be changed.

If selection is introduced in such a way that the ratio of fitness of behaviors i and j is $1:1 - s$, the phenogenotypic frequencies after selection are as follows:

$$\begin{aligned}Wx''_1 &= x'_1 \\Wx''_2 &= x'_2(1 - s) \\Wx''_3 &= x'_3 \\Wx''_4 &= x'_4(1 - s),\end{aligned}$$

where $W = 1 - x'_2s - x'_4s$.

The system has only two equilibria, one where A is fixed and the other where a is fixed. For this reason, we have examined the stability of one genotype near fixation to the introduction of the other genotype. The genotype a is not stable to the introduction of genotype A if

$$(\delta_a - \delta_A)(W(1 - s\beta_{ij}) - (1 - s)) < 0,$$

where W is the average fitness of a population with the genotype a fixed, and

$$\begin{aligned}W &= 1 - s((1 - \beta_{ij})(1 - \delta_a)x_3 + (1 - \beta_{ij} - \beta_{ij}\delta_a)x_4) \\&= 1 - s(1 - \beta_{ij} + \beta_{ij}\delta_a) + s\delta_ax_3,\end{aligned}$$

but $W(1 - s\beta_{ij}) - (1 - s)$ is greater than 0 because it is true for $x_3 = 0$. Thus,

$$1 - \beta - (1 - \beta_{ij} + \beta_{ij}\delta_a)(1 - s\beta_{ij}) > (1 - \beta_{ij})\beta_{ij}(1 - \delta_a) > 0,$$

and for $x_3 = 1$

$$(1 - s\beta_{ij})(1 - \beta_{ij})\delta_a > 0.$$

Then we can conclude that genotype a will always be invaded by genotype A because $\delta_A > \delta_a$; however, genotype A will also be stable against invasion by genotype a .

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