



# Modeling Imitation and Emulation in Constrained Search Spaces

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1 **Modeling imitation and emulation in constrained search spaces**

2

3 **Alberto Acerbi\*<sup>1</sup>, Claudio Tennie<sup>2</sup>, and Charles L. Nunn<sup>3</sup>**

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5 <sup>1</sup> Centre for the Study of Cultural Evolution - University of Stockholm

6

7 <sup>2</sup> Max Planck Institute for Evolutionary Anthropology - Department of Developmental and  
8 Comparative Psychology – Leipzig

9

10 <sup>3</sup> Department of Human Evolutionary Biology - Peabody Museum - Harvard University

11

12 \*author for correspondence:

13 Alberto Acerbi

14 Centre for the Study of Cultural Evolution - University of Stockholm

15 Lilla frescativägen 7B – 10691 Stockholm

16 phone: +46 08 163955

17 [alberto.acerbi@gmail.com](mailto:alberto.acerbi@gmail.com)

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21 RUNNING HEADLINE: Modeling imitation and emulation

22 **Abstract**

23 Social transmission of behavior can be realized through distinct mechanisms. Research on primate  
24 social learning typically distinguishes two forms of information that a learner can extract from a  
25 demonstrator: copying actions (defined as imitation), or copying only the consequential results (defined  
26 as emulation). We propose a decomposition of these learning mechanisms (plus individual learning)  
27 that incorporates the core idea that social learning can be represented as a search for an optimal  
28 behavior that is constrained by different kinds of information. We illustrate our approach with an  
29 individual based model in which individuals solve tasks in abstract “spaces” that represent behavioral  
30 actions, results, and benefits of those results. Depending on the learning mechanism at their disposal,  
31 individuals have differential access to the information conveyed in these spaces. We show how  
32 different classes of tasks may provide distinct advantages to individuals with different learning  
33 mechanisms, and discuss how our approach contributes to current empirical and theoretical research on  
34 social learning and culture.

## 35 **1. Introduction**

36 Imitation and emulation are two of the most commonly researched social learning mechanisms,  
37 especially in studies of primates (Call, Carpenter & Tomasello 2005; Hopper et al. 2007; Horner &  
38 Whiten 2005; Tennie, Call & Tomasello 2009). Several definitions of imitation and emulation exist in  
39 the literature. Here, we define emulation as the copying of the results, or environmental outcomes of  
40 demonstrations (i.e., the products of behavior), and imitation as the copying of the actions of a  
41 demonstrator (i.e., the behavioral processes leading to the products; Call & Carpenter 2002; Whiten,  
42 McCuigan, Marshall-Pescini & Hopper 2009; Tennie, Call & Tomasello 2006; Tomasello & Call 1997;  
43 Whiten, Horner, Litchfield & Marshall-Pescini 2004).

44         The differences between imitation and emulation may have profound implications for the  
45 capacity and scope of cultural transmission. In particular, it has been proposed that the capacity to  
46 reliably copy the actions of a demonstrator could make cumulative culture, technology and complex  
47 cultural behaviors possible, as is the case in humans, while non-human ape cultures may be better  
48 referred to as “traditions” (Galef 1992; Tomasello 1996). A reason for this difference is that emulation  
49 learning may be too inaccurate for a cultural ratchet to operate (Richerson & Boyd 2005; Shea 2009;  
50 Tennie et al. 2006, 2009; Tomasello 1999; compare also Whiten & van Schaik 2007). In fact, while  
51 imitation potentially results in the preservation of both process and product with a close one-to-one  
52 relationship between the two, emulation, by focusing only on the product or environmental effects, may  
53 lead to a failure in the preservation of the processes (Tennie et al. 2009).

54         To help understand the distinction between emulation and imitation, it is useful to consider a  
55 concrete task. For example, consider the specific task of tying a certain type of knot, and imagine  
56 individuals use different learning mechanisms. Emulators and imitators have access to information  
57 provided by a knowledgeable individual they observe, while individual learners do not have socially  
58 mediated information to guide their actions. If an individual is an emulator, she might have information  
59 about the form of the knot when it is completed, but she is “blind” to the process that produced the

60 knot. In order to arrive at the desired knot, the emulator may perform a series of actions with the rope  
61 without guidance and eventually “compare” her result with the observed knot. By comparison, if the  
62 individual is an imitator, she has additional information on the intermediate behavioral steps (more or  
63 less fine-grained) needed to produce the knot. She could use this information to guide her actions.  
64 Finally, individual learners have neither type of social information available. They rely only on self-  
65 evaluation of the effects that their own actions achieve.

66 In what follows, we present an individual based model that investigates the consequences of  
67 using imitation, emulation and individual learning. The model is based on the core idea that social  
68 learning can be represented as a search for an optimal behavior that is constrained by different kinds of  
69 information. Crucially, our approach differs from most other theoretical models that investigate cultural  
70 dynamics using mathematical tools developed in population genetics and epidemiology, which  
71 typically treat the transmission of cultural traits as analogous to the transmission of genetic material  
72 (starting from Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981). Such models tend to focus  
73 on dynamics at the population level, whereas behavior at the individual level, i.e., with respect to social  
74 learning processes, is only loosely described. In these models, “cultural transmission” is usually a  
75 process that involves a simple “transfer” of a behavior between individuals, with some probability  
76 attached to this transfer (e.g. Nunn, Thrall, Bartz, Dasgupta & Boesch 2009). Moreover, very few  
77 quantitative models explicitly consider how different social learning mechanisms can influence the  
78 diffusion of a behavior in a population. In one noteworthy exception, Kendal J.L., Kendal R.L. &  
79 Laland K. (2007) used a mathematical model to distinguish between stimulus enhancement and  
80 observational learning.

81 In our model, individuals solve various tasks described in abstract spaces that represent  
82 behavioral processes (actions), environmental outcomes from the behavior (results), and benefits of the  
83 actions. We refer to these as *actions space*, *results space* and *benefits space*, respectively. Depending  
84 on the learning mechanism at their disposal (imitation, emulation, and individual learning), individuals

85 have differential access to the information conveyed in these spaces, with imitators using both actions  
86 and benefits spaces, emulators using both results and benefits spaces, and individual learners using only  
87 benefits space. We illustrate how differently shaped spaces represent different classes of tasks, and,  
88 with our model, we show that these classes provide different advantages for the three learning  
89 mechanisms that we investigated. In an extension of the main model we consider chains of individuals  
90 that learn iteratively from one another. This model draws inspiration from the linear transmission chain  
91 method used in cultural learning research and we therefore call it the “transmission chain  
92 model”(Mesoudi & Whiten 2008). The model allows us to check whether an initial optimal behavior  
93 can be transmitted and maintained across generation using either imitation or emulation. Moreover,  
94 since in the iterative learning process the initial optimal behavior can get “lost”, we can test the effect  
95 of sub-optimal demonstrators on the two social learning mechanisms. In the last section, we discuss the  
96 relevance of our results to cultural evolutionary modeling, current experimental studies, and the  
97 relationship between social learning mechanisms and the evolution of human culture.

98

99

## 100 **2. Methods**

101

### 102 ***2.1 The search space***

103 A task can be described as involving a certain number of actions to be accomplished ( $N_a$ ). For each  
104 action a certain number of different variants ( $N_v$ ) is allowed. One can consider all possible behaviors as  
105 points in this  $N_a$ -dimensional *actions space*. The number of dimensions represents the number of  
106 actions needed to accomplish the task, while the size of each dimension represents the number of  
107 variants that are allowed for that specific action. To illustrate our approach, we use a simple actions  
108 space, with  $N_a=2$  and  $N_v=15$ . In other words, a task can be accomplished by using the right  
109 combination of two actions, and each of the two actions is chosen from fifteen possible different

110 variants (giving  $15^2$  possible combinations). Different combinations of these two actions (i.e., any  
111 determined point in the actions space) are considered different behaviors. We call the actions in the  
112 first dimension “action X” and the actions in the second dimension “action Y.”

113         The actions space has a correspondence in the *results space* (see Fig. 1 right panels). Here, for  
114 each point in the actions space (i.e., for each possible behavior) a result may (or may not) be present,  
115 where a “result” refers to an environmental modification that is similar to the observed one. Depending  
116 on the task at hand, some fraction of the environmental modifications may fail this criterion, which is  
117 why not all behaviors lead to results. Again it is useful to think of tying a knot: some combination(s) of  
118 actions can bring the rope to a physical configuration that is perceived by the individual as similar to  
119 the observed knot, while other combinations of actions leave the rope in a configuration perceived as  
120 non-matching, and thus not considered to be a result.

121         The actions space and results space have a final correspondence in the *benefits space* (see Fig.1  
122 left panels). Here, each behavior that produces a result also produces a net benefit. Note that the same  
123 result can have different benefits depending on the specific combination of actions used to obtain it.  
124 The underlying logic is that some actions combinations may be more effective than others, even if the  
125 result appears to be the same. These differences in benefits could arise because one action is less costly  
126 than another, as might occur if actions vary in time or energy needed for completion. Consider, for  
127 example, printing out several pages from a long word processing document versus writing them out by  
128 hand. The hand-written document would take much longer to produce and would be of lower quality,  
129 resulting in higher costs and lower benefit. In what follows, we simply use the term “benefit” referring  
130 to net benefits, i.e. benefits minus costs.

131         Together, the actions space, the results space, and the benefits space form the overall search  
132 space in which individuals search for optimal behavior. Individuals with different learning mechanisms  
133 access different spaces when solving problems – and thus can be “blind” to other spaces. Individual  
134 learners have only the benefits space at their disposal. Social learners can additionally make use of

135 information produced by a demonstrator in the actions space (for imitators) and in the results space (for  
136 emulators). Thus, the three learning mechanisms differ in their access to information conveyed by  
137 different spaces.

138

## 139 **2.2 Experimental conditions: different types of tasks**

140 To illustrate how the different learning mechanisms can give different advantages to individuals, we  
141 conceived three experimental conditions that correspond to different classes of tasks. We call the  
142 conditions *smooth task*, *peaked task*, and *hidden plateau task*. In all three conditions, there is a single  
143 optimal behavior, that is, a single point at which individuals obtain maximum benefit ( $b_{max}=1$ ), as  
144 shown in Figure 1.

145 In the *smooth task* (see Fig.1, a-b), action combinations lie on a linear gradient of benefits. The  
146 closer an action combination is to the single optimum, the higher is the benefit that this combination  
147 gives to the individual. Furthermore, all action combinations that give benefit to individuals produce  
148 the same result. Such tasks might characterize behaviors for which, first, even if a best possible  
149 solution exists, it is only of relative importance to perform *exactly* the highest rewarding combination  
150 of actions and, second, similar actions combinations give similar benefits to individuals. An example of  
151 a smooth task could be learning to catch a prey. The result (the prey caught) is always the same, but  
152 different action combinations may be more or less effective (e.g. involving more or less effort).  
153 Individuals may copy how knowledgeable demonstrators hunt but they can also try different action  
154 combinations and possibly self-evaluate the benefits obtained.

155 In the *peaked task* (see Fig. 1, c-d), only one single combination provides results as well as  
156 benefits. Unlike the smooth task, performing action combinations close to the single optimum in the  
157 peaked task does not produce any result and provides no benefit to the individual. For this family of  
158 tasks it is important to perform the *exact* combination of actions. Such tasks might characterize  
159 complex combinations of behavior involved in highly technical activities, where slight deviations from



160 a specific protocol lead to a failure in producing a result. To further elucidate the features of a peaked  
161 task, consider again the example of tying a knot. For some knots, if one performs action combinations  
162 that are *similar* but not identical to the correct combination needed to tie them, these will produce  
163 neither any usable result nor any tangible modification of the environment.

164 In the third and last condition, the *hidden plateau task* (see Fig. 1, e-f), only the single optimal  
165 combination provides benefits, but performing action combinations similar to the single optimal one  
166 produce results that appear to be correct. Such tasks might again represent highly technical behavioral  
167 activities, but in this case, a single correct combination occurs among closely related behaviors that  
168 produce comparable results. Once more we can refer to the knot example: for some type of knots, if the  
169 individual performs action combinations similar to the correct one, she can obtain some physical  
170 configuration of the rope similar to the knot of interest. Even if ineffective as a knot (i.e., benefits are  
171 zero), the result gives some indication that it is “close” to the optimal behavior.

172

173 **- FIG. 1 about here -**

174

### 175 ***2.3 The learning mechanisms***

176 Individuals perform searches with the aim of finding the optimal behavior on the search space. At each  
177 time step, an individual may modify her behavior by moving in the search space to adjacent actions  
178 combinations or may retain her previous behavior.

179 We model this search as a two-stage process. In the first stage, a possible modification of  
180 behavior is selected using the following rule: with respect to the current position of the individual, one  
181 of the two adjacent horizontal cells (action X) or one of the two adjacent vertical cells (action Y) is  
182 randomly selected as a possible new action, which would thus lead to a new behavior. This  
183 modification rule makes two assumptions: individuals can change only one action variant at a time  
184 (either X or Y), and individuals do not have access to all the possible action variants of this type in the

185 whole space, but only to a subset of two neighboring variants. The underlying rationale is that  
186 individuals likely experiment with actions that are somewhat similar to those they performed most  
187 recently. Note that this rule holds for all types of learners, so we are assuming a general “innovation”  
188 rule that underlies all types of learning.

189 In the second stage, individuals accept or discard the action modifications from stage one. If  
190 they discard the new action, they stay in the same point of the action space they were in before stage  
191 one, i.e. their behavior does not change. If they accept the new action, they will show a different  
192 behavior in the next time step. Three specific learning rules are used, depending on the learning  
193 mechanisms that individuals have at their disposal. Social learners make this decision by exploiting  
194 information from an “ideal” demonstrator who is performing the correct behavior at  $b_{max}$  on the space.

195 (1) Individual learners accept a new action if it does not reduce the benefit they were obtaining;  
196 otherwise, they discard the new action. Thus, individual learners always accept beneficial or neutral  
197 modifications. The assumption is that individual learners are able to quantify the net benefits of  
198 different actions and compare these benefits through time.

199 (2) Imitators base their decisions on how well the actions match the actions performed by the  
200 demonstrator. If they are already performing one of the demonstrator's action variants, they accept the  
201 modification only if they would then keep performing the same variant; otherwise they discard the  
202 newly selected action. For example, if an imitator already correctly performs the demonstrated action X  
203 (but not the action Y), she will not change her position with regard to the action X, but she will accept  
204 any modification on the action she uses from the action Y. If imitators are not performing any of the  
205 two demonstrator's action variants they always accept every modification. The assumption underlying  
206 this rule is that imitators initially lack knowledge of how to perform an action, but they can compare  
207 their actions with those of the demonstrator.

208 (3) Emulators base their decisions on whether the result is obtained (i.e., gray areas of Fig. 1,  
209 right panels). In contrast to imitators, emulators are blind to the actions of the demonstrator, but they do

210 have information on the result. If emulators are already obtaining the demonstrator's result they accept  
211 the proposed modification only if they keep obtaining the same result; otherwise, they discard it (in a  
212 way logically comparable to imitators). In contrast, if they have not yet obtained the demonstrator's  
213 result they always accept modifications. The assumption is that emulators do not know how to obtain a  
214 result, but they know how well their result matches the demonstrator's result.

215 As noted above, social learners are likely to also make decisions based on the net benefits that  
216 they obtain. Thus, in our model, imitators and emulators also make use of the benefits space. More  
217 specifically, they use the benefits space to guide their decisions when the information provided by the  
218 demonstrator can not be used to orient their search, i.e. when they accept the random behavior in the  
219 first stage of the behavioral modification rule (this procedure is analogous to the “critical social  
220 learner” in Enquist, Eriksson & Ghirlanda, 2007).

221

## 222 ***2.4 Simulations procedures***

223 For each of the three conditions, we tested  $10^4$  individuals for each learning mechanism (imitation,  
224 emulation, and individual learning), giving  $3 \cdot 10^4$  simulations for each condition, for a total of  $9 \cdot 10^4$   
225 simulations. At the beginning of the simulation each individual is placed randomly in the actions space  
226 (i.e., she has a random behavior) and the simulation runs until the individual reaches the behavior that  
227 produces the maximum benefit ( $b_{max}=1$ ). We collected output on the individual benefit through time  
228 and on the time it took the individual to reach  $b_{max}$  (i.e., the time step in which she performed the  
229 optimal behavior). We also recorded the number of time steps in which social learners made use of the  
230 benefits space information, rather than using the information provided by the demonstrator (results or  
231 actions).

232 In a second set of simulations we sketched a possible extension of the main model that  
233 simulates multiple generations of individuals (“transmission chain model”). We focused only on two  
234 conditions (peaked task and hidden plateau task) and on the two social learning mechanisms (imitation

235 and emulation) without considering pure individual learning. At the beginning of the transmission  
236 chain simulation, a single individual with random behavior learns from a knowledgeable demonstrator  
237 that shows the optimal behavior. After a certain number of time steps the learning phase ends and the  
238 observer, regardless of her behavior, now becomes the demonstrator for a newly introduced naïve  
239 individual. Differently from the main model, in the transmission chain model the demonstrator may  
240 thus show a sub-optimal behavior. In this case, if the observer succeeds in copying the demonstrator's  
241 behavior without reaching  $b_{max}=1$  (meaning that behavior is sub-optimal), the observer continues to  
242 explore the search space using individual learning, until she reaches  $b_{max}=1$  or the learning phase ends.

243 We iterated this process for 100 generations, varying the length of the learning phase from 100  
244 to 1000 steps (incremented in units of 100) and comparing the results of imitation and emulation for the  
245 2 conditions. This involved a total of 40 simulations (2 conditions X 2 learning mechanisms X 10 sets  
246 of learning steps), which we replicated 1000 times. We collected output on the benefit at the last  
247 generation and on the individual benefit through generations.

248

249

## 250 **3. Results**

### 251 *3.1. Main model*

252 In the smooth task condition, the effectiveness of the three learning mechanisms was similar in terms of  
253 average benefits through time and in the average length of time required to reach  $b_{max}$  (Fig. 2, a).  
254 Individual learners exploited the benefits gradient to orient their search for optimal behavior, and social  
255 learning appeared to provide no advantages relative to individual learning. Thus, we found that social  
256 learners generally behaved as individual learners, meaning that they made use of the benefits space  
257 rather than the information (actions or results) provided by the demonstrator. Imitators used the  
258 benefits space in 77% ( $\pm 18$  SD) of the time steps, showing that in the majority of cases, social  
259 knowledge was not informative in their search for the optimal behavior. Emulators used benefits space

260 more often than imitators ( $98\% \pm 3$  SD).

261 In contrast to the smooth task condition, in the peaked task condition, imitation outperformed  
262 both emulation and individual learning (Fig. 2, b). In this task, the benefits and results spaces did not  
263 contain information useful to emulators and individual learners; hence, emulators and individual  
264 learners basically performed a random search, resulting in a longer average time to find  $b_{max}$ . Imitators  
265 were advantaged because they exploited information on the actions of the demonstrator to orient their  
266 search.

267 Lastly, in the hidden plateau task, both types of social learners outperformed individual learners  
268 (Fig. 2, c). Imitators were again advantaged over individual learners, as seen in the peaked task. In the  
269 hidden plateau task, emulators also experienced advantages relative to individual learners, but they  
270 benefited in a different way from imitators. While imitators gained advantages by homing in on the  
271 specific actions to use, emulators used the “plateau” of close results too orient their search (see Fig. 1,  
272 e). Importantly, this plateau is “hidden” to individual learners and imitators.

273

274 **- FIG. 2 about here -**

275

276 To understand the differential performance of imitators and emulators it is useful to think about  
277 how individuals with different learning strategies view the spaces in terms of attractors (Fig. 3), and  
278 specifically how they use information to move through the space. Imitators move in the space as if they  
279 can attach to the “cross-hairs” of a target. Once they land on a correct action, they move randomly  
280 along the axis defined by this action until they reach the other correct action (Fig. 3, a). In contrast, the  
281 emulators' attractor is the area of the space in which they obtain the demonstrator's result (Fig. 3, b).  
282 Once in the plateau, they move randomly on the plateau until they find the optimum.

283

284 **- FIG. 3 about here -**

285

286           As seen in Figure 3, the relative size of the plateau is likely to determine the effectiveness of  
287 emulation relative to other learning mechanisms. To assess this effect, we ran additional simulations of  
288 emulators in the hidden plateau task in which we varied the dimensions of the results plateau. Results  
289 are shown in Figure 4. If the area is relatively small (as in the peaked task) the plateau is difficult to  
290 find, reducing the effectiveness of emulation. Similarly, if the plateau is relatively large (as in the  
291 smooth task) emulation is also less effective because finding the plateau does not provide much useful  
292 information to the agent. Finally, for intermediate sizes (as in our hidden plateau task) emulation can be  
293 as effective as imitation.

294

295

**- FIG. 4 about here -**

296

### 297 *3.2. Transmission chain model*

298

299 In the transmission chain model, the learned behavior was iteratively transmitted across generations of  
300 individuals. Our simulation of this process produced results that were largely congruent with those  
301 found in the main model. Thus, in the peaked task condition (Fig. 5, a), chains of imitators  
302 outperformed chains of emulators. Given a sufficient duration of the learning phase (approximately  
303 from 500 steps), imitation was effective in transmitting the initial optimal behavior across generations.  
304 Emulation was never as effective as imitation in the peaked task, and, even for relatively long learning  
305 phases (e.g. 1000 steps), chains of emulators never achieved the optimal behavior at the end of the  
306 iterative process (i.e. the average final benefit never reached 1). In the hidden plateau condition (Fig. 5,  
307 b), however, the two social learning mechanisms were equally effective in transmitting the optimal  
308 behavior across generations, provided an adequately long learning phase (i.e. greater than about 500  
309 steps).

310

311

- FIG. 5 about here -

312

313           The duration of the learning phase has two effects on learning dynamics. At the level of the  
314 single individual, short learning phases translate in lower probabilities to acquire the correct behavior  
315 from the demonstrator. At the level of inter-generational transmission, however, this effect is amplified  
316 by the fact that, across generations, naïve individuals have sub-optimal demonstrators. The two effects  
317 can be shown considering the case of imitation in the peaked task condition (Fig. 6). Learning phase of  
318 100 and 300 steps produced an initial disadvantage at generation 1 (effect at individual level). This  
319 disadvantage was amplified across generations. By comparison, for the case of a learning phase of 500  
320 steps, the optimal behavior is maintained across generations.

321

322

- FIG. 6 about here -

323

#### 324 **4. Discussion**

325 Our results illustrate how different learning mechanisms may provide individuals with different  
326 advantages depending on the type of task at hand, and they suggest that different behavioral diffusion  
327 dynamics can be generated under different learning mechanisms. Specifically, real-world tasks  
328 comparable to our smooth task can be solved effectively using individual learning, since the benefits  
329 gradient provides a way to orient search behavior. In nonhuman apes, such a situation might be found  
330 in gorilla “nettle feeding” behavior, which involves neutralizing stinging hairs on nettle leaves (a plant  
331 food source). The task space here is indeed likely to be smooth: given extended practice, many actions  
332 can be tried, their relative effectiveness evaluated, and individuals can thus learn how to optimize the  
333 process of neutralizing stinging hairs efficiently. We therefore expect that individual gorillas adjust  
334 their actions so that individuals (and even populations) converge on the same behavior. Indeed, even

335 though social learning of an imitation type was first proposed as a candidate to equip subjects with the  
336 necessary skill (e.g. Byrne & Russon 1998), it was recently found in captive settings that individual  
337 learning (likely together with genetic predispositions) is a more parsimonious explanation (Tennie,  
338 Hedwig, Call & Tomasello 2008).

339 In contrast, our findings indicate that imitation is especially useful for solving peaked tasks.  
340 Such tasks not only require the chaining of correct actions (in a correct sequence), but they also provide  
341 little or no feedback for performing behaviors other than the optimal one (here we assumed no  
342 feedback was provided). Individuals thus cannot orient their search in any way other than by copying  
343 the actions of a demonstrator. In real-life human culture, many tasks are likely to fit this description,  
344 including using cognitively opaque artifacts, learning a gestural language, or performing correct  
345 performances of religious rituals or dances (see Tennie et al. 2009).

346 Finally, emulation can provide advantages in situations analogous to our hidden plateau tasks,  
347 where emulators may take advantage of the fact that performing actions similar to the correct one  
348 produce a result. Even if the result is ineffective (i.e., benefit is zero), the plateau of results can give  
349 emulators guidance towards achieving the optimal behavior.

350 These results are confirmed in an extension of the model (“transmission chain model”) where  
351 we considered the effectiveness of social learning mechanisms when individuals learn iteratively across  
352 generations. In particular, imitation can maintain an optimal behavior through generations regardless of  
353 which kind of tasks is at hand (peaked task or hidden plateau task), while emulation, even when  
354 individuals can learn for relatively more time steps, is unable to preserve good solutions to problems  
355 presented by peaked tasks, which are frequent in human culture (see above).

356 Different social learning mechanisms are rarely differentiated in cultural evolution models  
357 (Mesoudi 2009), yet our results show that specific dynamics are generated through interactions of the  
358 tasks and learning mechanisms used. Modeling social learning as a general mechanism of behavioral  
359 transfer can hide this important interplay. Including specific modeling of social learning mechanisms



360 (as done here) seems advisable in order to help distinguish between social and asocial learning  
361 diffusion dynamics (Franz & Nunn 2009; Kendal et al. 2007; Kendal, Kendal, Hoppit & Laland 2009;  
362 Hoppit, Boogert & Laland 2010; Reader 2004), as well as for models explicitly dedicated to the study  
363 of social learning in animals or, more broadly, to the evolution of cultural capacities (Nunn et al. 2009;  
364 van Schaik & Pradhan 2003; Whitehead 2007). The case of human culture can be different because the  
365 extensive use of imitation and teaching (Gergely & Csibra 2006; Tomasello 1999) can render social  
366 learning reliable enough to generally interpret behavioral diffusions as genuine “transmission”  
367 processes. However, it could also be the case that a selective switching of social learning mechanisms  
368 could generate different dynamics in humans. For example, the distribution of artifacts in the  
369 archaeological record suggests a need to explain patterns not only in terms of population level biases  
370 (e.g. Mesoudi & O'Brien 2008) but also in terms of different mechanisms of learning at the individual  
371 level (Tehrani & Riede 2008).

372         Our model could provide new insights to the results of animal behavior studies concerning the  
373 distinction between imitation and emulation. In particular, the results of our model help to better define  
374 which kind of tasks may give rise to an imitative strategy. Many scientists agree that the “difficulty” of  
375 a task can represent an important variable in determining which social learning mechanism an  
376 individual will potentially use, with “easy” tasks readily solved by individual learning but  
377 “challenging” tasks better solved by imitation (see Tennie et al. 2009; Whiten et al. 2009). In our  
378 model, a “challenging” task is represented by the peaked task and the challenge arises from the absence  
379 of feedback for performing behaviors similar to the correct one. For animal behavior studies this means  
380 that experimental tasks with these particular features are needed to determine whether a species can and  
381 does use imitation. Successful social learning in tasks with smooth structures or hidden plateau  
382 structures could be explained with mechanisms other than imitation, while, on the other hand, the  
383 *absence* of imitation in solving those tasks can be due to the search structure rather than an intrinsic  
384 limitation of the species’ imitative ability. This is not to say that a species capable of imitation would

385 only imitate in tasks that have this type of structure. A species able to imitate might use this learning  
386 strategy in a wider range of contexts. For example, humans also imitate in types of tasks for which  
387 other strategies would be equally useful or even better (see above and Horner & Whiten 2005; Tennie  
388 et al. 2006). This phenomenon has recently been dubbed "over-imitation" (Lyons, Young & Keil 2007),  
389 and it seems to hold cross-culturally (Nielsen & Tomaselli, 2010).

390 Finally, our results offer some considerations regarding the relationship between general  
391 intelligence, the rarity of imitation in primates, and the evolution of culture. In a peaked task, the ability  
392 to reliably copy the actions of a demonstrator is, in our model, much more effective than emulation and  
393 individual learning. Humans face this kind of task repeatedly throughout life and they readily use  
394 imitation to solve these tasks, while this class of tasks is probably uncommon in other primates (Tennie  
395 et al. 2009). Hence, the problems that non-human primates confront in the wild are characterized by an  
396 interaction between genetic predispositions and environmental feedback which may effectively orient  
397 their "search" without the need to copy the specific actions of a demonstrator (van Schaik & Pradhan  
398 2003; Tennie et al. 2009, Tennie, Call & Tomasello 2010), and the same may have been true of some  
399 early hominin artifacts (e.g. handaxes, compare also Richerson & Boyd 2005).

400 Perhaps non-human primates do not imitate because socio-ecological conditions have not  
401 favored imitation. The learning mechanisms available to them suffice. However, when solutions to  
402 problems in the form of peaked structures started to be invented and provided marked fitness  
403 advantages to individuals, selection for imitative learning likely increased. This suggests that the initial  
404 diffusion of task solutions in the form of peaked structure created an environment that boosted the  
405 pressure to develop imitative skills (i.e., niche construction effects, see Laland, Odling-Smee &  
406 Feldman 2000). Widespread imitation in a given population could be used to support a process of  
407 cumulative culture that, in turn, opens up new fitness landscapes involving technological innovations  
408 which are likely to create "complex" solutions to adaptive problems perhaps in the form of peaked  
409 structures, which then favor greater imitative learning ability.

410           It is important to be clear about several simplifications that we made in this first investigation of  
411 the modeling framework. First, we assumed that for each condition only a single optimal behavior  
412 existed (for a coverage of multimodal adaptive landscapes in cultural evolution see Boyd & Richerson  
413 1992; Mesoudi 2008). Second, we assumed a “perfect demonstrator” who, from the beginning and  
414 reliably, performed the optimal behavior (but note that in the transmission chain model this behavior  
415 could get “lost” through the iterative process and so this model is relatively free from such problem).  
416 Third, we assumed that all learning mechanisms have the same implementation costs. As a final issue,  
417 it is important to stress that we deliberately omitted several psychological aspects that influence  
418 learning processes, including memory and cognitive constraints. The two-stage process of behavioral  
419 modification that we used should not be viewed as an accurate model of real behavioral learning  
420 processes. For example, we are not claiming that real-life imitators actually perform novel behaviors  
421 quasi-randomly and that they then “compare and discard” them if different from a demonstrator’s  
422 behavior. We consider our approach as a modeling device (and thus necessarily and intentionally  
423 minimalistic) to illustrate the aspect we stated in the introductory section, namely, that social learning  
424 can be interpreted as a search for an optimal behavior constrained by different kind of information in  
425 the social context, and moreover, that different tasks can be modeled as information spaces that have  
426 different shapes.

427           In summary, our model illustrates a new framework for interpreting social learning mechanisms  
428 that could hopefully be incorporated in cultural evolutionary modeling. The model also suggests  
429 directions for new experiments, shows that the structure of a task is crucial for the interpretation of  
430 experimental outcomes, and proposes a framework to characterize different experimental tasks.  
431 Moreover, the highlighted interplay between a learning mechanism’s effectiveness and features of  
432 different tasks suggest some considerations on the relationship between general intelligence, the ability  
433 to imitate, and the evolution of cultural capacities.

434

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436

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439

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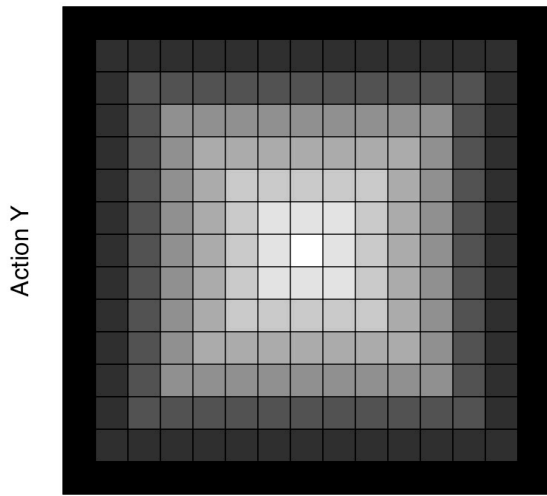
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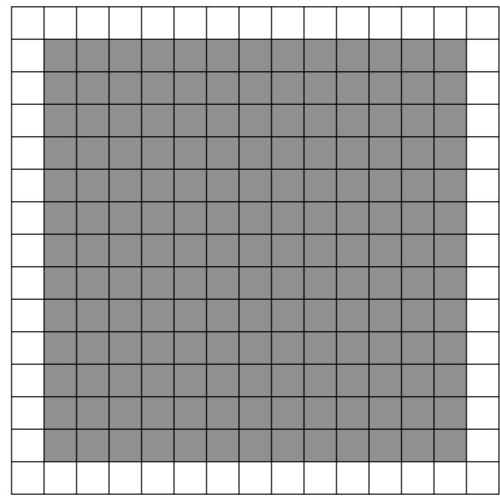
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571 **Figure 1: Features of benefits spaces (left) and results spaces (right) in the three experimental**  
572 **conditions.** Each point on the X- and Y-axes show a particular variant for X and Y actions (i.e., actions  
573 space). From top to bottom, panels show smooth task, peaked task, and hidden plateau task. For  
574 benefits spaces, benefits goes from  $b=0$  (black) to  $b_{max}=1$  (white). For results spaces, gray color  
575 represents points in which individuals obtain a result and white color points in which they do not obtain  
576 a result.

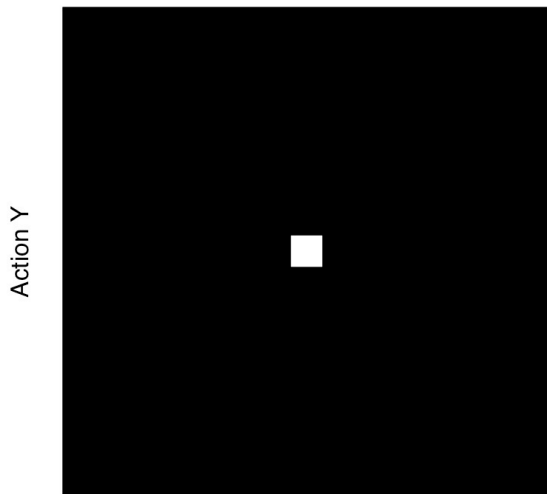
a. Smooth task (Benefit space)



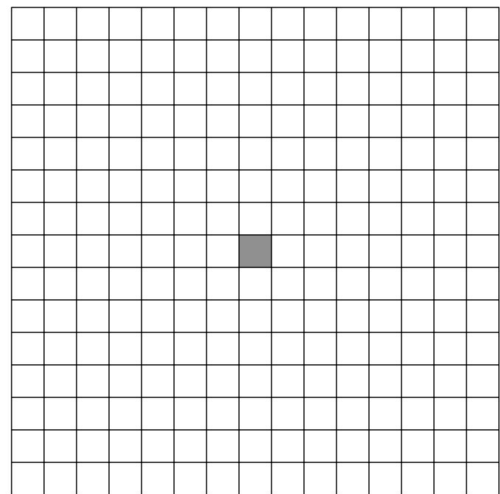
b. Smooth task (Result space)



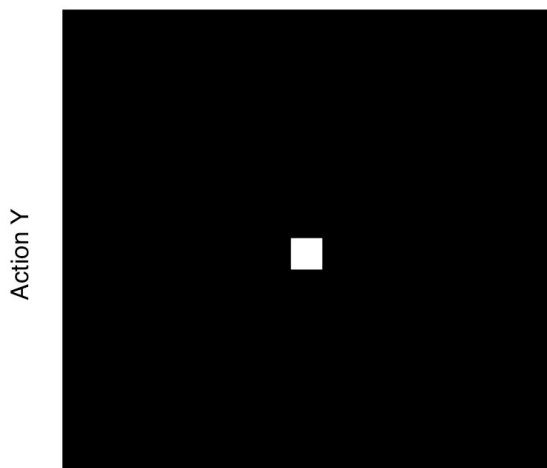
c. Peaked task (Benefit space)



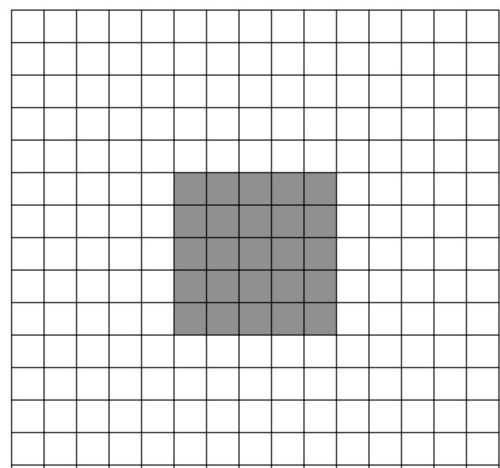
d. Peaked task (Result space)



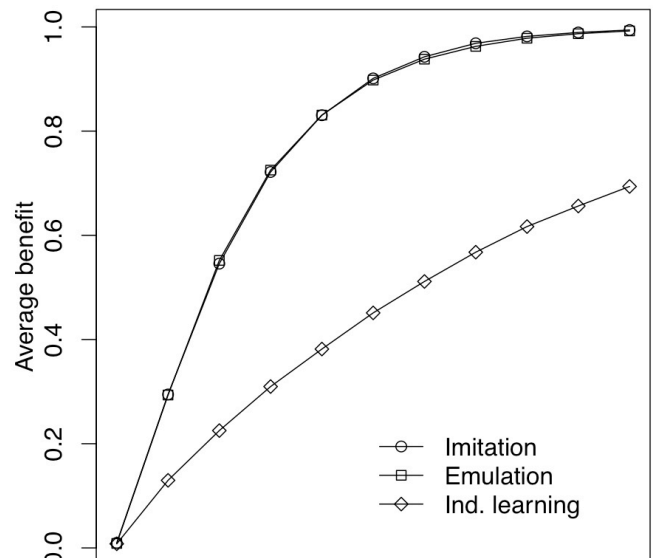
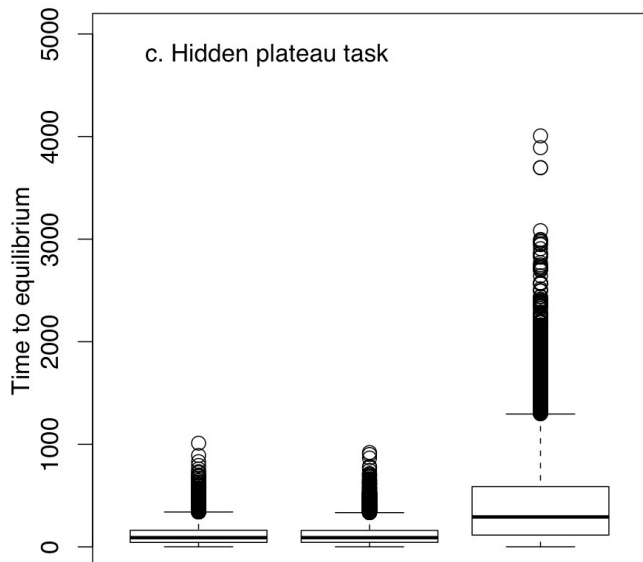
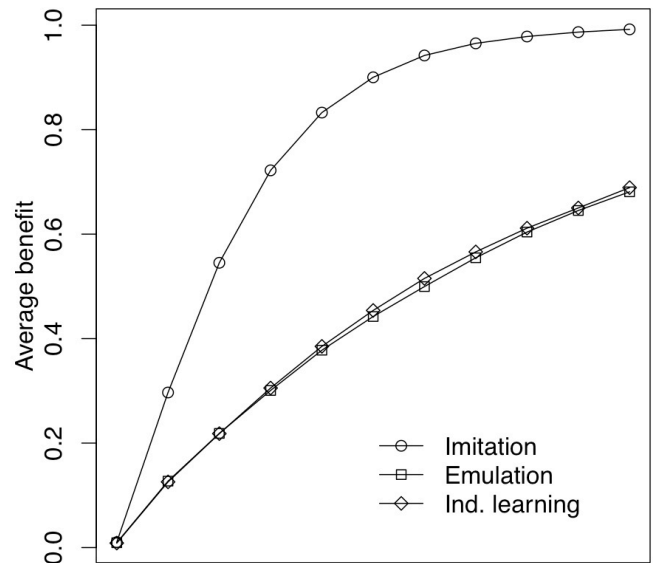
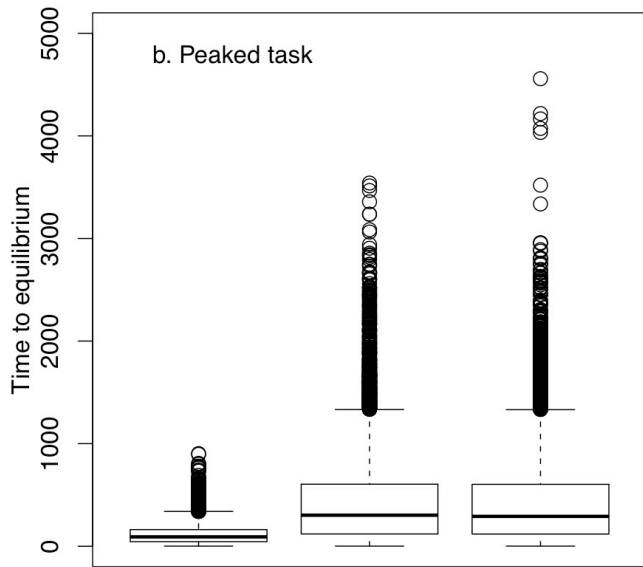
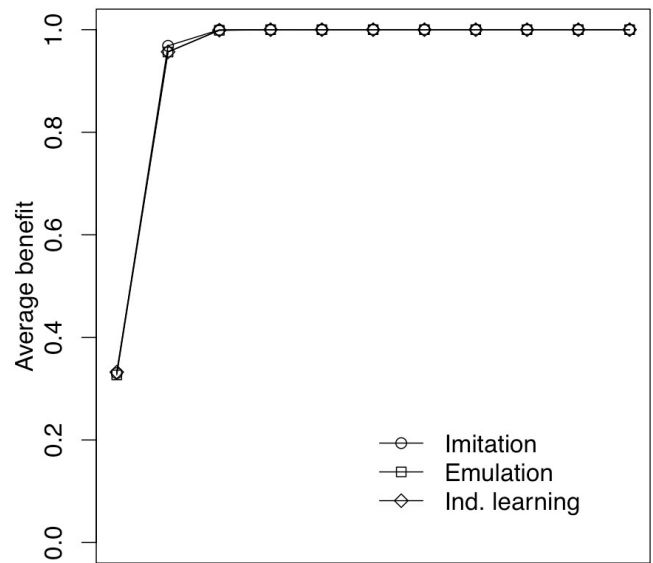
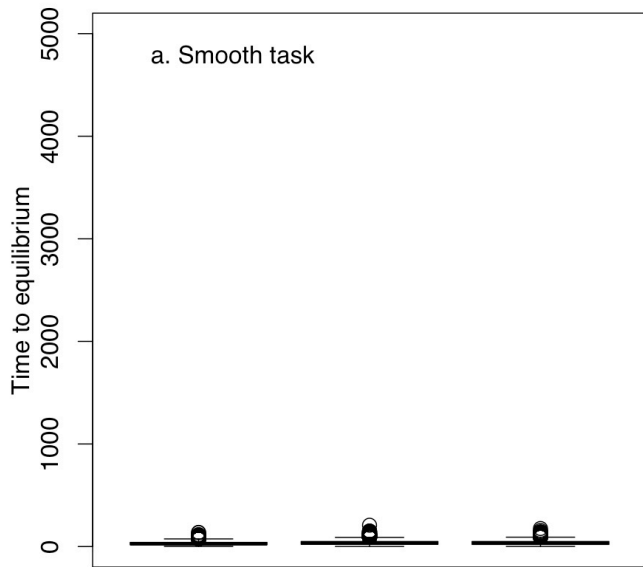
e. Hidden plateau task (Benefit space)



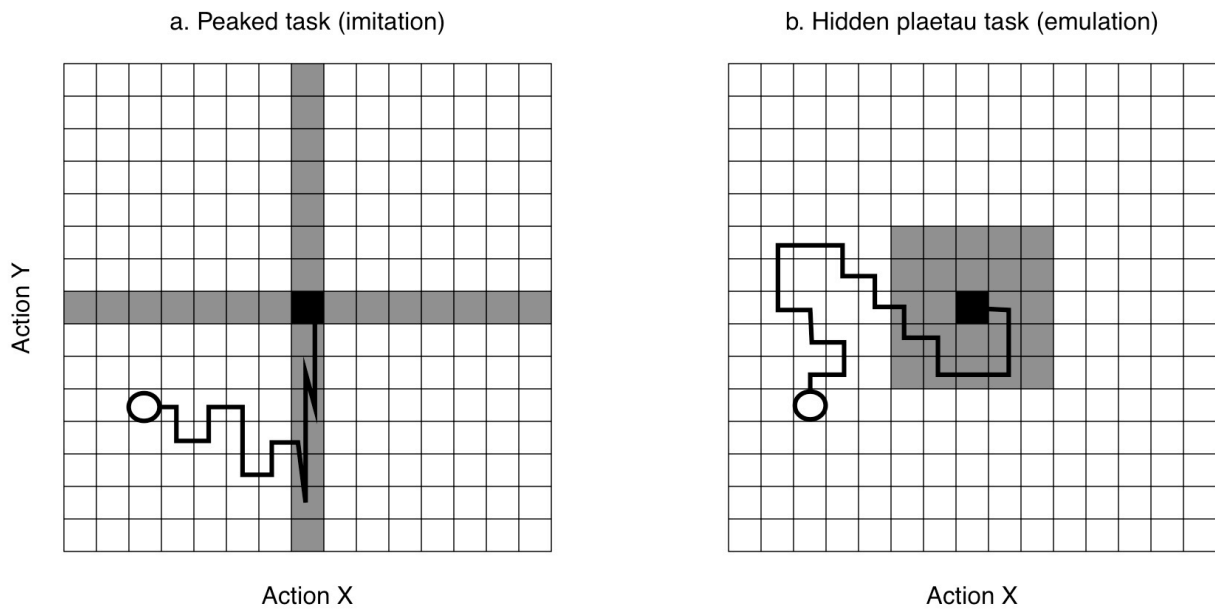
f. Hidden plateau task (Result space)



578 **Figure 2: Synthesis of results of the main model.** From top to bottom, panels show smooth task  
579 condition, peaked task condition, and hidden plateau task condition. Left panels: Time steps until  
580 individuals reach  $b_{max}=1$ . Boxes represent the inter-quartile range of the data. The horizontal lines  
581 inside the boxes indicate the median values. The horizontal lines outside the boxes indicate the  
582 minimum and maximum values not considered outliers. Circles represent outliers. Right panels:  
583 Average benefits (on  $10^4$  individuals) in the first 500 time steps. Circles = imitation. Squares =  
584 emulation. Diamonds = individual learning.



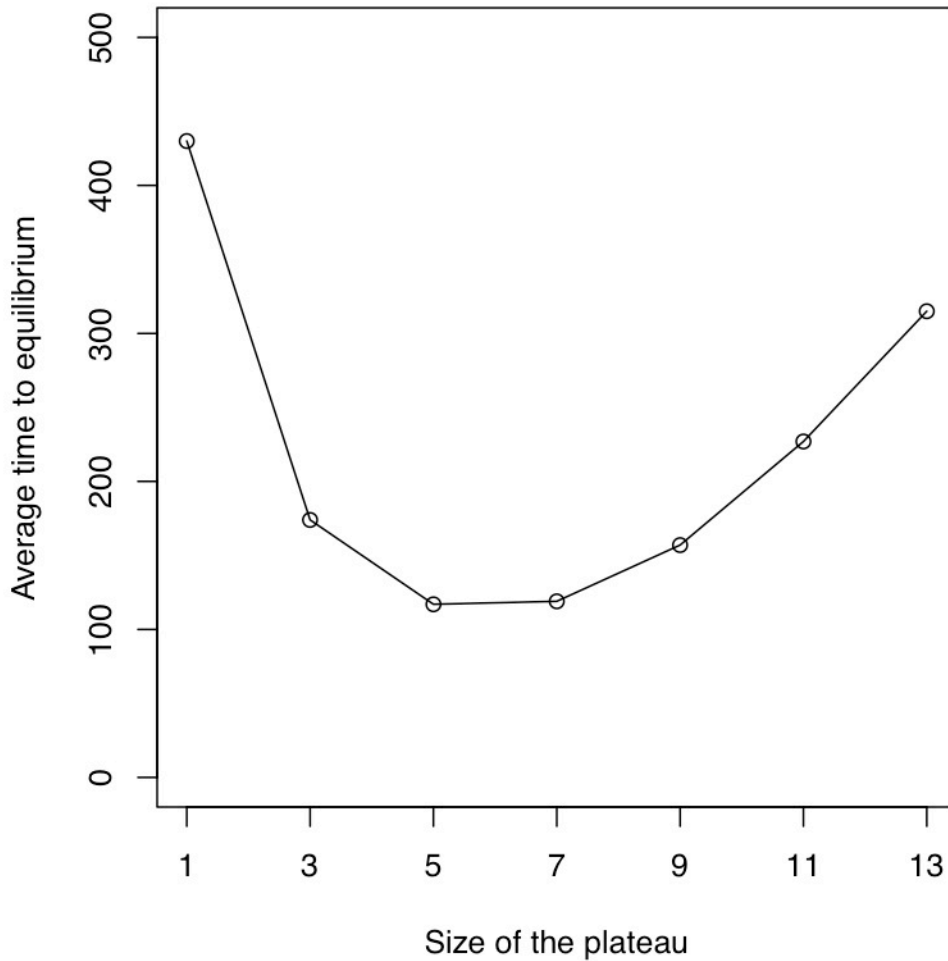
586 **Figure 3: Space attractors for imitators (a) and emulators (b).** The black square represents the  
587 optimal behavior in the search space, while the dark gray squares represent the behavioral attractors.  
588 (a): Hypothetical trajectory of an imitator searching for the optimal behavior in the peaked task  
589 condition. After the individual arrives in the “crosshairs,” she only accepts moves that keep her in the  
590 crosshairs. Thus, the crosshairs serve as an attractor. (b): Hypothetical trajectory of an emulators  
591 searching for the optimal behavior in the hidden plateau task condition. In this case, the plateau is the  
592 attractor. Thus, when an emulator lands in the plateau, she only accepts moves that keep her in the  
593 plateau.



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602 **Figure 4: Effectiveness of emulation when varying the size of the results plateau in the hidden**  
603 **plateau task.** Average time steps until emulators reach  $b_{max}=1$  in the hidden plateau task versus  
604 dimension of the results plateau. The dimension of the results plateau is expressed as the length of the  
605 side of the results area (a square). In the main simulation this length is equal to 5 points in the results  
606 space (see Figure 1-f).



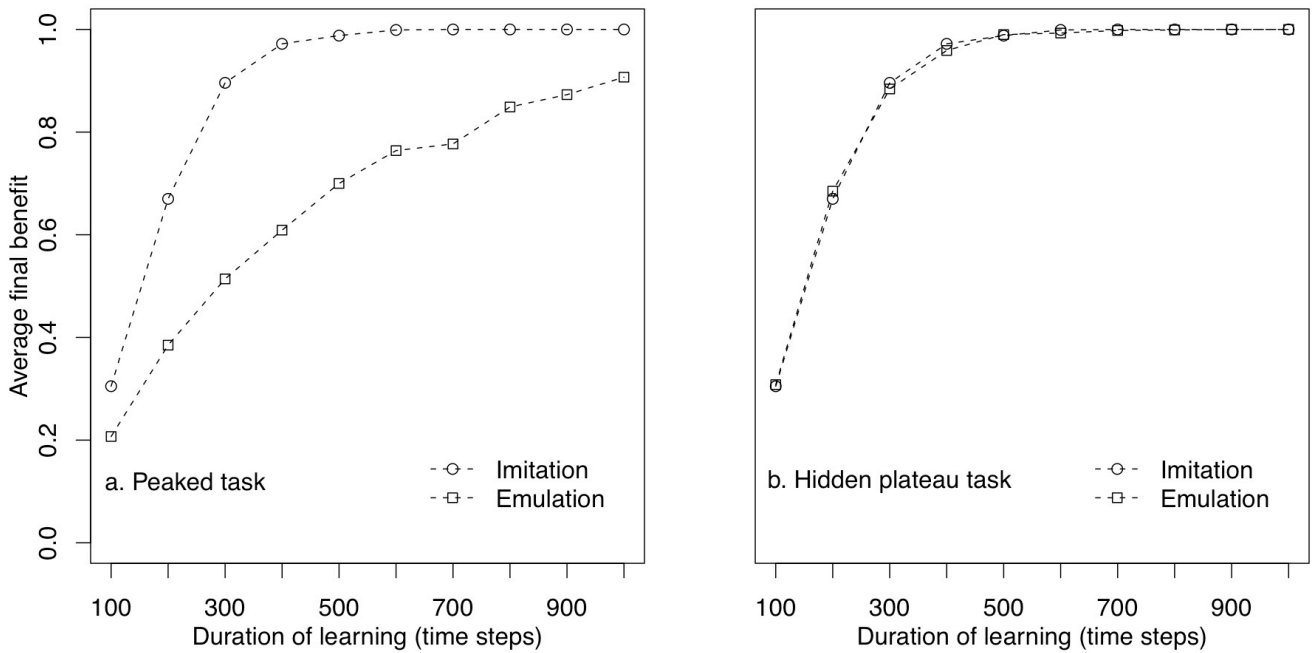
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611 **Figure 5: Synthesis of results of the transmission chain model.** Average final benefit (on 1000  
612 replications) versus duration of the learning phase. Circles = imitation. Squares = emulation. (a):  
613 peaked task condition. (b): hidden plateau task condition.



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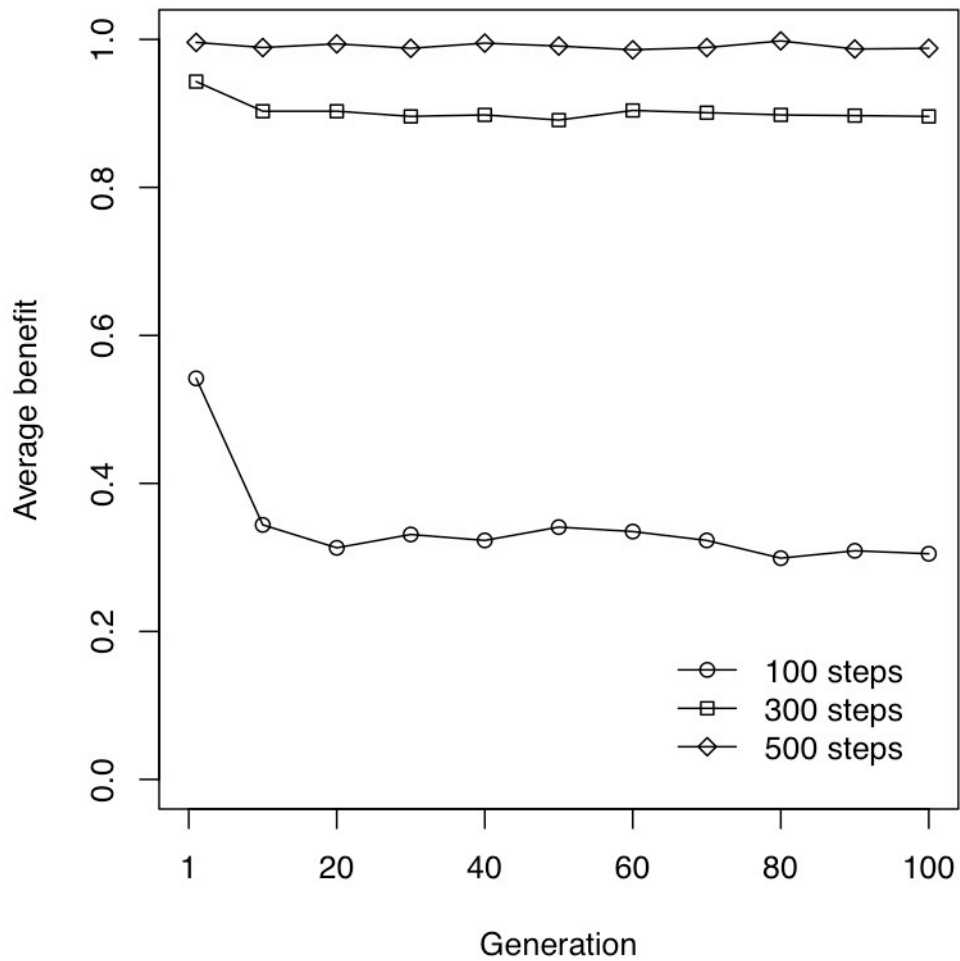


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627 **Figure 6: Effectiveness of imitation across generations (peaked task condition).** Average benefit  
628 across generations for imitators with different durations of the learning phase in the peaked task  
629 condition. Circles = 100 time steps. Squares = 300 time steps. Diamonds = 500 time steps.



630