



**HAL**  
open science

## The experimental emergence of convention in a non-human primate

Anthony Formaux, Dany Paleressompoulle, Joël Fagot, Nicolas Claidière

► **To cite this version:**

Anthony Formaux, Dany Paleressompoulle, Joël Fagot, Nicolas Claidière. The experimental emergence of convention in a non-human primate. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2021, 377, 10.1098/rstb.2020.0310 . hal-03549748

**HAL Id: hal-03549748**

**<https://hal.science/hal-03549748v1>**

Submitted on 31 Jan 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# The experimental emergence of convention in a non-human primate

Anthony Formaux<sup>1,2</sup>, Dany Paleressompouille<sup>1</sup>, Joël Fagot<sup>1,2,3</sup>, Nicolas Claidière<sup>1,2,3\*</sup>

1 – Aix Marseille Univ, CNRS, LPC, Marseille, France

2 – Station de Primatologie-Celphedia, CNRS UAR846, Rousset, France

3 - Institute for Language, Communication and the Brain, Université Aix-Marseille, CNRS, Aix-en-Provence, France.

\* - Correspondance to : Nicolas Claidière, Laboratoire de Psychologie Cognitive, UMR7290, Université Aix-Marseille/CNRS, 13331 Marseille, France. Email: [nicolas.claidiere@normalesup.org](mailto:nicolas.claidiere@normalesup.org)

OrcidID : Anthony Formaux (0000-0001-7857-2349), Joël Fagot (0000-0002-9824-9685), Nicolas Claidière (0000-0002-4472-6597)

1

## 2 1. Summary

3 Conventions form an essential part of human social and cultural behaviour and may also be  
4 important to other animal societies. Yet, despite the wealth of evidence that has accumulated for  
5 culture in non-human animals, we know surprisingly little about non-human conventions beyond a  
6 few rare examples. We follow the literature in behavioural ecology and evolution and define  
7 conventions as systematic behaviours that solve a coordination problem in which two or more  
8 individuals need to display complementary behaviour to obtain a mutually beneficial outcome. We

9 start by discussing the literature on conventions in non-human primates from this perspective and  
10 conclude that all the ingredients for conventions to emerge are present and therefore that they  
11 ought to be more frequently observed. We then probe emergence of conventions by using a unique  
12 novel experimental system in which pairs of Guinea baboons (*Papio papio*) can voluntarily  
13 participate together in touch-screen based cognitive testing and we show that conventions readily  
14 emerge in our experimental setup and that they share three fundamental properties of human  
15 conventions (arbitrariness, stability and efficiency). These results question the idea that  
16 observational learning, and imitation in particular, is necessary to establish conventions, they  
17 suggest that positive reinforcement is enough.

18 **Keywords: primate social cognition, social learning, animal culture, language evolution,**  
19 **imitation**

## 20 **2. Introduction**

21 Conventions form an essential part of human social and cultural behaviour and may also be  
22 important to other animal societies. Yet only a few rare examples of conventions have been  
23 documented (see Stephens & Heinen, 2018 for a discussion of non-human conventions), despite the  
24 existence of evolutionary precursors (Kappeler, Fichtel, & van Schaik, 2019). The first part of this  
25 article discusses current evidence of conventions in non-human primates and concludes that  
26 conventions ought to be more frequently observed. The scarcity of convention has been explained  
27 by the limited social learning capacities of non-human primates, especially regarding imitation.  
28 However, in the second part of the article we present a set of experiments showing the emergence  
29 of convention in a non-human primate using a unique novel experimental system. These  
30 experiments show that Guinea baboons (*Papio papio*) can readily develop conventions that share at  
31 least three properties of human conventions (arbitrariness, stability and efficiency) through simple  
32 reinforcement learning. We start by clarifying the meaning and properties of convention.

33 Intuitively conventions are rule-like behaviour such as shaking hands as a greeting. Beyond  
34 this intuitive understanding however, conventions have proven difficult to define and have been  
35 much debated. Here, we will follow a 'Lewisian' approach (Lewis, 1969) and define conventions as  
36 systematic behaviours that solve a coordination problem in which two or more individuals need to  
37 display complementary behaviour to obtain a mutually beneficial outcome.

38 A classic example of convention, used by Hume (1888) and taken up by Lewis, is that of two  
39 rowers on a boat. If both rows are synchronized, the boat will move forward smoothly, whereas if  
40 they row out of sync, it will behave erratically. In Hume's (then Lewis's) use, this example illustrates  
41 the main properties of convention: 1) rowers do not keep promises to act in concert, 2) they may  
42 express their shared interest explicitly, but not necessarily, 3) to row in rhythm, there must be a  
43 gradual installation of synchronous behaviour, 4) they may know that what is being set up between  
44 them is a convention, but not know how to describe it verbally ("We start at the 90° angle and give  
45 a stroke every 2 seconds") and 5) they have adopted a rhythm that they keep because it works, but  
46 there are alternatives. We discuss some of these characteristics in more detail below.

47 Individuals can find *ad hoc* solutions to coordination problems when they arise, as when  
48 finding seating arrangements around the table for instance. However, when coordination problems  
49 happen regularly and/or impose a high cost for a failure to coordinate, individuals may benefit from  
50 establishing a convention (Hawkins & Goldstone, 2016). Notice that compared to other types of  
51 positive interactions such as helping (one individual benefits at the expense of another) or  
52 cooperation (individuals can benefit more by being selfish), individuals mutually benefit from  
53 coordination: it is in their own best interest and in the interest of the partner(s) to coordinate.  
54 Therefore, there is no conflict of interest between individuals when solving a coordination problem  
55 or when establishing a convention. Rather, conventions are important because they help stabilize  
56 interactions by creating mutual expectations between individuals. Someone picking up his/her car  
57 in France expects other individuals to drive on the right side of the road and so adjusts his/her  
58 behaviour accordingly. These expectations need not be explicit nor mutually acknowledged for a

59 convention to exist (Moore, 2013). In fact, sometimes we are barely aware that a convention exists:  
60 you might lunch at a certain time simply because you expect other people to lunch around that  
61 time. According to Hawkins' theoretical model (2019), three processes allow the emergence and  
62 maintenance of a convention: the population level (social network management and cultural  
63 transmission), the dyad level (coordination and social interaction) and the individual level (executive  
64 functions and expectations). A convention is not necessarily created as a result of a problem  
65 encountered by the whole population at one point. If enough dyads in the population repeatedly  
66 encounter a coordination problem and each individual belongs to several dyads, a population-wide  
67 convention can emerge.

68         Of course, a paradigmatic example of convention in humans is language because to  
69 communicate individuals need to coordinate on word-meaning relationships. Studies have shown  
70 how humans can develop new conventions to communicate during the natural emergence of new  
71 languages such as pidgin (which occurs when individuals with no common language need to  
72 communicate, Bickerton, 1981) or sign language (for instance the Nicaraguan sign language for  
73 example, Kegl, 1994) and these studies have been complemented by experiments and models  
74 showing how conventions develop during the emergence of artificial communication systems (Fay,  
75 Garrod, Roberts, & Swoboda, 2010; Galantucci, 2005). Conventions are traditionally distinguished  
76 from habits and norms. Habits are patterns of individual behaviour that do not (strongly) depend on  
77 other individuals, but they can be shared and cultural: taking a shower vs. taking a bath for instance.  
78 In contrast, norms may be seen as solving coordination problems when the interest of individuals  
79 are not aligned. They are associated to a sense of "oughtness" and punishment that conventions  
80 and habits lack, e.g. "crossing at a red light" (e.g. Bicchieri, 2005). Clearly, given the diversity of  
81 human social behaviour, there are no strict boundaries between habits, conventions, and norms.  
82 What was once a habit, "spitting in the street", can become a norm "do not spit" (Nichols, 2002).  
83 Conventions, e.g. "crossing at pedestrian crossings" can be felt to some like norms that ought to be  
84 followed at all times and by others as mere conventions. There are also habits, "eating cheese

85 before dessert”, that, although not a coordination problem *per se*, are easier to deal with when  
86 everyone follows the same rules (e.g. to have a meal together). Therefore, conventions are not an  
87 “all or nothing” kind of thing but a “more or less” one: behaviours are more or less conventional  
88 depending on how closely they match the prototypical example of convention.

89 In the framework of game theory (Deming, Neumann, & Morgenstern, 1944), a coordination  
90 problem is a problem with multiple Nash equilibriums (a strategy is a Nash equilibrium when no  
91 player can do better by changing his strategy alone; (Nash, 1951)) and a convention is a Nash  
92 equilibrium to such problem (see Lewis (1969) for the original discussion and Stephens and Heinen  
93 (2018) for a more detailed discussion in the context of animal behaviour). The Nash equilibrium, i.e.  
94 the convention, is governed by initial conditions and dynamics (influenced by the way individuals  
95 choose to act and the environment). Note that conventions require multiple equilibriums because if  
96 there are no alternative options, there would be no coordination problem to solve in the first place  
97 and two individuals would necessarily converge on the unique solution. However, different  
98 equilibriums need not be equally rewarding, one may lead to higher rewards for instance (called  
99 payoff dominant strategies) and some equilibriums may be more rewarding than others when  
100 individuals deviate from the equilibrium (risk dominant equilibrium). Note that in the framework of  
101 game theory a convention is ‘arbitrary’ because there are multiple Nash equilibriums to a  
102 coordination problem, so a population could have ended up using another convention. It does not  
103 mean that individuals are arbitrarily choosing one behaviour over another, they may strategically  
104 choose a payoff dominant strategy for instance. Importantly, compared to their one-shot  
105 counterpart, repeated economic games can help create conventions because with repetition  
106 multiple equilibriums often appear (Fudenberg & Maskin, 2008).

107 To summarise, when individuals regularly face coordination problems, they may develop  
108 conventions as solutions to these problems. Conventions are systematic behaviours that are  
109 mutually beneficial and provide stable expectations about other individuals. Thus conventions, like  
110 norms, help individuals stabilize their social environment and navigate their social world. It is

111 important to note that conventions do not require individuals to do the same action (one could pull  
112 while the other pushes), they can concern as few as two individuals, and they do not necessarily  
113 lead to the optimal solution (other more profitable equilibria may exist). Conventions are usually  
114 associated with three important properties (Hawkins & Goldstone, 2016):

- 115 1. **Arbitrariness:** at least one alternative exists and would be equally acceptable if everyone  
116 coordinated on it.
- 117 2. **Efficiency:** individuals benefit from establishing a convention.
- 118 3. **Stability:** over multiple games behaviour converges towards an attractor.

119 Conventions are the natural outcome of individuals repeatedly facing coordination problems  
120 together and are therefore expected in group-living animals and especially in tightly bonded non-  
121 human primates. Recently, Stephens et al. (2018) reviewed evidence of conventions in non-human  
122 animals using a game-theoretic perspective but did not discuss primates, and Kappeler et al. (2019)  
123 provided an important analysis of the evolutionary behavioural, emotional and cognitive precursors  
124 of norms and conventions in non-human primates. Here, we complement this work by discussing  
125 specific cases of non-human primate behaviour in the context just discussed that is graded and  
126 grounded in a game-theoretic perspective.

### 127 **3. Conventions in non-human primates?**

128 Susan Perry and colleagues' description of social conventions in white-faced capuchin  
129 monkeys (*Cebus capucinus*) is one of the best description of conventions we have in non-human  
130 primates (Perry et al., 2003). Using 13 years of data collection in their field sites in Costa Rica, Perry  
131 et al. describe the fashion-like emergence of new behaviour. During *hand-sniffing* for instance (first  
132 reported by Fedigan, 1993) two individuals are resting together and one individual holds the hand  
133 or foot of another over its own face. These behaviours are similar in many respects to human  
134 conventions such as shaking hands: they require coordination between pairs of individuals because  
135 individuals need to be together and to perform complementary behaviour, emerge in some groups

136 and not others and can spread to a large proportion of individuals within the group. They can also  
137 stay stable for a long time, in one group hand-sniffing was observed during seven years before  
138 disappearing. Finally, these behaviours could have a function close to our handshakes because they  
139 may strengthen the bonds between individuals. These behaviours therefore appear to have all the  
140 properties of conventions. Similarly, the *hand-clasp* grooming (McGrew, Marchant, Scott, & Tutin,  
141 2001; van Leeuwen, 2021; van Leeuwen, Cronin, Haun, Mundry, & Bodamer, 2012) and *social-*  
142 *scratch* grooming of chimpanzees (Nakamura, McGrew, Marchant, & Nishida, 2000) also appear to  
143 meet the requirements of conventions: they are stable behaviour that solve coordination problems  
144 for which alternative behaviour exist. In addition, the social structure may vary between groups of  
145 the same species and some behaviours may be considered conventional under the definition  
146 proposed here. For example, van de Waal (2018) showed that neighbouring groups of vervet  
147 monkeys differ in the structure of their social networks as well as how they handle conflict. When  
148 conflicts arise within a group, alternative behaviours can be adopted to bring back stability, some  
149 groups adopt affiliative behaviours (conciliation or reconciliation) while others adopt agonistic  
150 behaviours (coalition or redirection). Another similar example is the emergence and transmission of  
151 a "pacific culture" within a troop of wild olive baboons (*Papio anubis*) (Sapolsky, 2006; Sapolsky &  
152 Share, 2004). Due to unfortunate circumstances, a large proportion of the most aggressive males of  
153 the troop died of tuberculosis, the few remaining males were untypically affiliative and non-  
154 aggressive, creating a troop with high rates of grooming and relaxed dominance hierarchy. The low  
155 level of aggression, compared to a neighbouring group residing in the same reserve, was stable and  
156 maintained in the group for over 20 years despite the migration of new individuals. These are good  
157 examples of convention, because different behaviours can be stable solutions to coordination  
158 problems (how to respect the dominance hierarchy for instance) and individuals benefit from a  
159 stable social organisation (social stability has important fitness benefits (Gilby et al., 2013; Schülke,  
160 Bhagavatula, Vigilant, & Ostner, 2010; Silk, 2007; Silk et al., 2009).



161 Notably, most social learning experiments (see Heyes, 1994 for a definition of social  
162 learning) do not result in the establishment of conventions, mostly because they do not involve  
163 coordination problems but individual solving abilities. For instance, in the classical study of Whiten,  
164 Horner, and de Waal (2005), chimpanzees can solve a puzzle box using two different techniques and  
165 they learn to do so by watching other individuals. Since only one individual solves the problem at a  
166 time, there is no coordination between them regarding the technique they use. It also emphasizes  
167 the difficulty of defining precisely what a convention is, and the fine line between social learning  
168 and convention studies.

169 Some social learning experiments however show suggestive evidence of conventionality. In  
170 the studies of van de Waal, Borgeaud, and Whiten (2013) for instance, groups of vervet monkeys  
171 (*Chlorocebus aethiops*) learned to eat food of one colour (e.g. pink) and avoid food from another  
172 colour (e.g. blue). Once this preference had been learned, results showed that monkeys continued  
173 to prefer to eat food of only one colour even when they were exposed to edible versions of both  
174 colours. Even more surprisingly, monkeys that migrated from one group (e.g. pink) to another (e.g.  
175 blue) sometimes adopted the behaviour of members of the group against their own previous  
176 preference (e.g. they switch from pink to blue). One possible explanation for the vervet monkeys'  
177 behaviour is that they needed to compete for food to establish their dominance within the group<sup>1</sup>.  
178 Indeed, dominance hierarchies are examples of conventions, they are stable solutions to  
179 coordination problems (to access food and/or reproduction) and provide stable expectations

---

<sup>1</sup> We thank Kate Arnold (University of St Andrews) for pointing this out to us.

180 regarding others' behaviour (see Bergman, Beehner, Cheney, & Seyfarth, 2003). In a particular  
181 group there certainly are several stable solutions to organise the dominance between individuals,  
182 that organisation is therefore conventional to some extent. However, the dominance hierarchy is  
183 also typical of a species and constrained by genetic dispositions and although it could be tempting  
184 to extend the concept of conventions to behaviour that are largely genetically determined  
185 (Stephens & Heinen, 2018), here we will limit ourselves to learned conventions.

186 This consideration is also important to determine if non-human primate communication is  
187 conventional. Non-human primates' vocalisations and gestures come from a largely fixed repertoire  
188 and are not conventional (e.g. Arnold & Zuberbühler, 2008; Kemp et al., 2017; Ouattara, Lemasson,  
189 & Zuberbühler, 2009; Tomasello & Zuberbühler, 2002). Although, note that conventions, in the form  
190 of geographical dialects, have been observed in other vocal-learning non-human species (e.g. Slater,  
191 1986; Weilgart & Whitehead, 1997) and that there is some limited evidence of vocal flexibility in  
192 non-human primates (Snowdon & Elowson, 1999; Watson et al., 2015). Watson et al. (2015) in  
193 particular observed the convergence of food calls during the integration of two chimpanzee groups  
194 over a three-year period.

195 In non-human primates, some flexible gestural communications can emerge through  
196 "ontogenetic ritualisation" (Tomasello & Call, 1997), a process through which an action at the  
197 beginning of an action sequence, such as raising an arm before play-hitting another individual,  
198 progressively becomes a signal to initiate the action sequence, raising an arm to initiate rough-and-  
199 tumble play (Tomasello, 2008). However, ontogenetic ritualisation does not systematically give rise  
200 to conventions because there is a direct link between the sequence of actions to perform and the  
201 signal that is used to initiate it, there is therefore no alternative signal through which this could be  
202 initiated (Moore, 2013). Chimpanzee and bonobo gestures overlap extensively in form and meaning  
203 for instance (Graham, Hobaiter, Ounsley, Furuichi, & Byrne, 2018). However, in one group of  
204 mandrills (*Mandrillus sphinx*) Laidre (2011) described the emergence of a novel *eye-covering*  
205 gesture probably used to signal that the individual was resting. This gesture was unique to this

206 group and had been observed for nearly a decade in the group and never seen elsewhere where  
207 other behaviours are used to signal 'resting' (such as lying down or turning one's back). Therefore,  
208 this signal may be seen as conventional to some extent, even if it is iconic. Interestingly, during the  
209 emergence of sign language when signals are created, they are initially iconic, motivated by features  
210 of the situated interaction. Later, iconic signals become arbitrary symbols as they are stylised and  
211 ritualised. This happens to the point that new learners use them without awareness of the initial  
212 motivation, and, in many cases, the initial iconic motivation is undetectable (Garrod et al. 2007).

213         Of course, the absence of conventions in non-human primates' communication contrasts  
214 sharply with human language that is often considered to be a paradigmatic example of convention  
215 since the word-meaning association is largely arbitrary (Lewis, 1969). Noteworthily, Tomasello  
216 (2008) has proposed that linguistic and other human conventions are learned by imitation and that  
217 the lack of a capacity for imitation in non-human primates could explain both their apparent lack of  
218 conventions and their lack of language (see also Moore, 2013). Tamariz (2019) goes further and  
219 argues that it is not imitation (copying goals and behaviour) but copying without paying attention to  
220 goals, that makes language uniquely human (Tamariz, 2019). For example, children first learn to  
221 reproduce the sound of a word before they learn the conventional way to use them.

222         The experiments we present below come to question the role of imitation in the  
223 establishment of conventions since we observe the emergence of convention in a non-human  
224 primate without imitation or other forms of observational learning. In our experiments two  
225 baboons are seated next to each other facing computer touchscreens and they can see each other's  
226 screen. When the experiment starts one baboon is randomly selected and must choose between  
227 two stimuli, then the next individual is presented with the same two stimuli and must choose one  
228 too. When the same two stimuli are selected, the two baboons are rewarded. Using this  
229 coordination task, we wanted to ask the following three main questions:

- 230 1. Will the baboons solve this coordination problem by developing a convention?  
231 Compared to choosing the stimuli independently or to responding by watching what the  
232 other individual selected.
- 233 2. If the baboons develop a convention, is observational learning necessary or important?  
234 3. If the baboons develop a convention, to what extent are they arbitrary and depend on  
235 the group social structure?  
236

## 237 **4. Method**

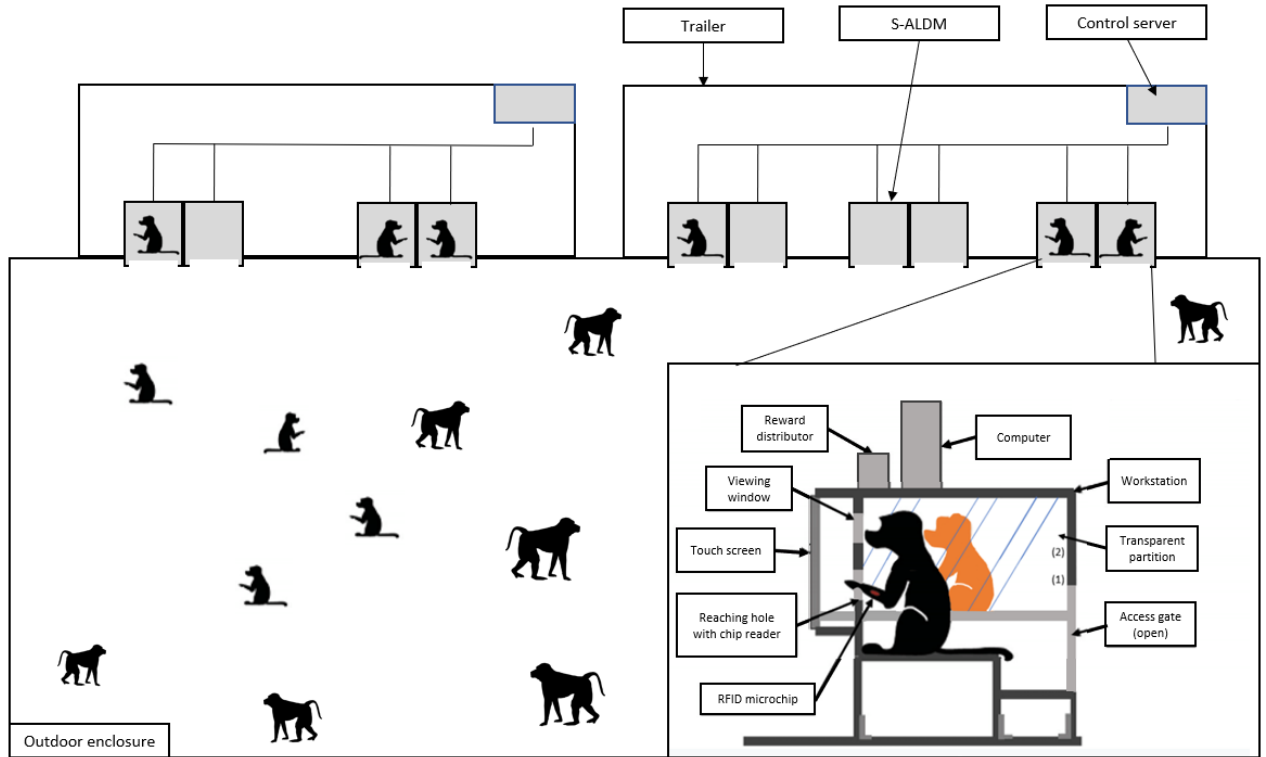
### 238 **Section 4.1 Participants**

239 Nineteen Guinea baboons (*Papio papio*, 13 females) from the CNRS primatology center in  
240 Rousset-sur-Arc were tested in this study (mean age: 12.2 years [min=3.25; max=25.3]). They  
241 belonged to a social group of 19 individuals living in a 25x30m outdoor enclosure connected to a  
242 6x4m indoor enclosure and two 8x4m trailers (Fig.1a). The monkeys had *ad libitum* access to five S-  
243 ALDMs (Social - Automated Computer Learning Devices for Monkeys; see below) four in the first  
244 trailer and six in the second.

#### 245 **Social Automated Computer Learning Devices for Monkeys (S-ALDMs)**

246 The ALDMs (Fagot & Bonté, 2010; Fagot & Paleressompouille, 2009) are operant conditioning test  
247 systems that can be used for testing non-human primates in social setting. ALDMs use an automatic  
248 radio frequency identification device implanted in each forearm of the monkeys to detect the  
249 location and identity of specific individuals. This device makes it possible to test the animals without  
250 having to capture and isolate them (additional information of the setup can be found in Fagot,  
251 Gullstrand, Kemp, Defilles, & Mekaouche, 2014; Fagot, Marzouki, Huguet, Gullstrand, & Claidière,  
252 2015). The ALDMs presented in Fagot et al. (2015) were modified in 2018 and connected in pairs to  
253 allow an individual in one ALDM to both see its partner and its touchscreen of the neighboring  
254 ALDM (see Fig.1b). We dubbed this new version of ALDMs the Social-ALDMs or S-ALDMs for short.

255 Two individuals could therefore see each other and their responses on the screen when a  
 256 transparent partition between the S-ALDM was used or they had no visual access when an opaque  
 257 partition was used. All the monkeys had previously participated in studies using this S-ALDM testing  
 258 system but had never performed the present experiment.



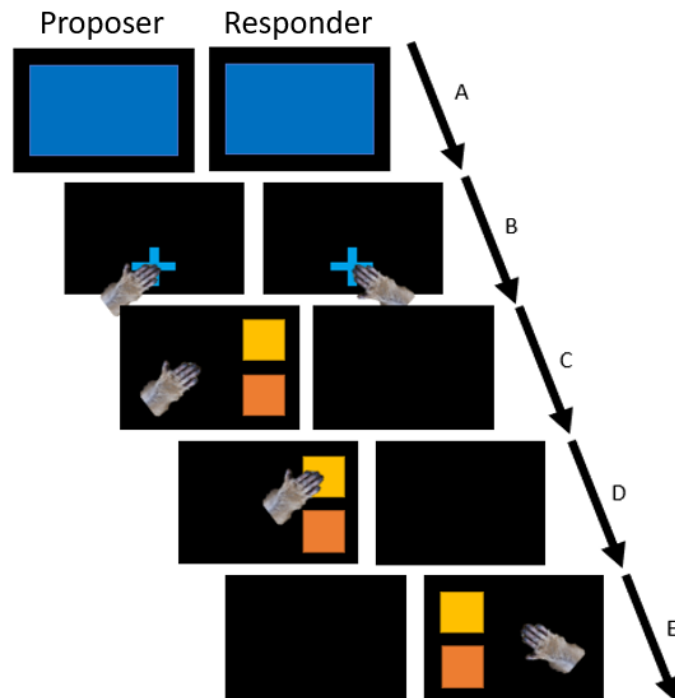
259  
 260 Figure 1: (a) 19 baboons living in an enclosure have *ad libitum* access to two trailers, each  
 261 containing several S-ALDMs. The diagram shows the two bungalows and the five units. (b) Detail of  
 262 the organization of a workstation, where two monkeys can work side by side, while seeing each  
 263 other.

264 **Computerised task**

265 We used two different tasks, one when two individuals are present, the “dual task”, and one  
 266 when an individual is alone, the “filler task”. These two tasks are presented below. When a monkey  
 267 entered an S-ALDM, a blue screen was displayed in its monitor with a 4-second delay. If another  
 268 individual was detected in the neighboring S-ALDM during this delay, a blue screen was also  
 269 displayed on the adjoining monitor, announcing the synchronization of the two machines and the  
 270 start of the dual task (Fig.2 and video in ESM). Otherwise, if the neighboring S-ALDM stayed empty

271 for 4 secs, the filler task started. The function of the filler task was mainly to keep the baboons  
272 occupied within the S-ALDM while waiting for another individual to arrive.

273 *Dual task*



274  
275 Figure 2: Schematic representation of the dual task on touch screen. A to E: succession of  
276 events.

277 During the dual task (Fig. 2), which is the focus of this paper, the test program identified the  
278 two monkeys when they entered an S-ALDM, synchronized the two computers, and displayed a blue  
279 fixation cross at the bottom center of both screens (Fig.2B). The test started once both monkeys  
280 had pressed the fixation cross and within a delay of 4-secs (otherwise the trial was aborted and re-  
281 presented). One monkey of the pair was then randomly selected. This first monkey, that we are  
282 going to call "proposer", had to choose between two randomly placed visual stimuli on the screen  
283 (Fig.2C). These stimuli were located on the side of the screen so that the second monkey, the  
284 "responder", had the best possible view. Once the stimulus was selected by the proposer, it would  
285 flash twice (Fig.2D), then both stimuli would disappear and appear on the responder's screen. The  
286 responder then had to choose one of the two stimuli according to what the neighbor had chosen  
287 (Fig.2E). If both proposer and responder selected the same target the trial was considered a success,

288 otherwise, a miss. The success of a test was coded as a binary variable: correct response = 1 and  
289 incorrect response = 0. A success triggered the delivery of a reward to the two individuals of the  
290 pair, a miss resulted in a 3 secs timeout for both. We presented experiments with seven or five  
291 different stimuli, therefore 21 or 10 possible different combinations. To balance all possible  
292 combinations the trials were organized in randomly ordered block of 42 (for seven stimuli) or 40 (for  
293 five) trials.

#### 294 *Filler task*

295 If a monkey presented itself at an S-ALDM and no other monkey participated in the task in  
296 the neighboring station (at the time of synchronization of the blue screens, see Fig. 2A), a version of  
297 the Wisconsin Card Sorting Task (WCST, Berg, 1948) was presented. The WCST is commonly used in  
298 executive control studies to assess cognitive flexibility and has been adapted to the ALDM system  
299 by Bonté, Flemming, and Fagot (2011). In the present study, the WCST was used as a filler task  
300 therefore these data will not be analyzed in the context of this paper.

#### 301 **Statistical analysis**

302 We used two measures to understand the emergence of conventions in our experiments.  
303 The first variable of interest is the score of individuals (i.e. whether they succeeded at the task and  
304 were rewarded) because it indicates if the monkeys are solving the coordination task. To analyse  
305 the score, we consider independently the score when an individual is in the role of the proposer,  
306 from the score when in the role of the responder. This is because the roles are very different, the  
307 proposer cannot respond based on visual information, the receiver can. Note that individuals can in  
308 principle have very different scores as proposer and responder, if one individual uses visual  
309 information and not another for instance. To understand the evolution of score over time we  
310 analyse the average score on a block of trials (40 or 42 trials, see above) performed by an individual.

311 To understand how the conventions emerge, we also used the Elo-score rating technique  
312 (Elo, 1978). The Elo-score is used to rank chess players and to analyse dominance hierarchies in  
313 animals for instance (Strauss & Holekamp, 2019). The advantage is that it is a dynamic index, when

314 a contest takes place, the Elo-score of the winner increases, while that of the loser decreases. In  
315 our case, we used the Elo-score package (Sánchez-Tójar, Schroeder, & Farine, 2018; see ESM and  
316 the analysis code for details) to represent the dominance between stimuli: every time a monkey  
317 chooses one stimulus over another, that stimulus ‘wins’, the other loses (the  $k$  parameter was set to  
318 1 and the initial elo-score was set at 0). The Elo-score technique therefore allows us to see if there is  
319 a hierarchy appearing during the experiment and to track changes in the hierarchy if they appear,  
320 which is important to assess stability.

321 We performed several experiments in which we manipulated the partition between  
322 individuals (either transparent or opaque) and the stimuli (all stimuli are freely available with the  
323 data and code to analyse the results). Since these experiments are based on the voluntary partition  
324 of monkeys, we could not control the number of trials done per individual or by pairs of individuals,  
325 so the number of blocks performed by individuals vary and we analyse only complete blocks. The  
326 evolution of Score with the number of blocks was evaluated using a generalized mixed linear model  
327 (GLMM, Baayen, Davidson, & Bates, 2008) with binomial error distribution and a logit link function.  
328 Models were analysed using the `stan_glm` function of R's `rstanarm` package (Goodrich, Gabry, Ali,  
329 & Brilleman, 2020) with default weakly informative priors as recommended. Convergence was  
330 checked using the `shinystan` package (Muth, Oravecz, & Gabry, 2018) and we found no convergence  
331 issues. To consider inter-individual variability and repeated measurement, we used mixed models  
332 including a random intercept and slope (represented by the number of blocks of 42 trials  
333 performed) for each individual. Thus, we limit our analysis to complete blocks of trials (all the model  
334 details are presented in the ESM). Additional analyses use nonparametric tests due to the non-  
335 independent nature of the data.

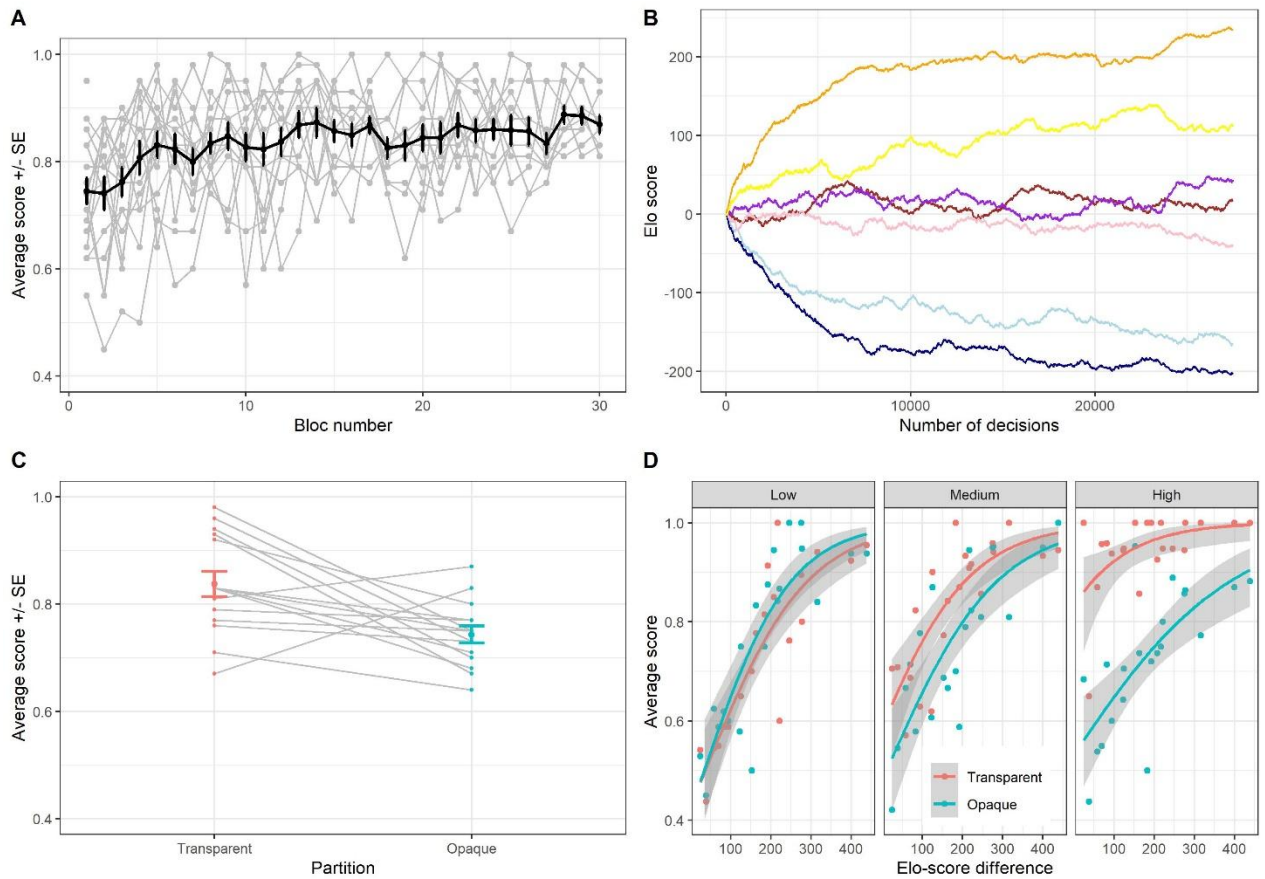
336 All analyses were done with the statistical software R (R Core Team, 2021).

## 337 **5. Study 1: stability of convention**



338 In this first study, the baboons had to choose between pairs of coloured stimuli from seven  
339 possible colours (see video 1 in ESM). During the first period of the experiment, monkeys could see  
340 each other's responses through the transparent partition between them. We start by focusing on  
341 the proposer whose role is to choose which of the two colours is to be selected. We found that the  
342 proposer's score was initially high (mean score for the first block = 0.75, SEM = 0.02, min = 0.55,  
343 max = 0.95) and steadily increased at the beginning of the experiment with the number of blocks ( $\beta$   
344 = 0.03, 95%CI = [0.02,0.04]; Fig.3A). This increase in score was linked to the establishment of a  
345 hierarchy between colours (Fig.3B), some colours (such as yellow and orange) became progressively  
346 more chosen by the proposer than others (such as light and dark blue). We found that at the end of  
347 the experiment (we used the last two blocks of trials for each proposer to get a reliable measure of  
348 score for every pair of colours) the difference in dominance rank between colours was highly  
349 correlated to the average score for that pair (Kendall, N = 21,  $\tau = 0.71$ ,  $z = 4.53$ ,  $p < 0.001$ ), for  
350 instance the probability of success when orange and dark blue were presented together was on  
351 average 99% (a difference in Elo-score of 316) while it was 60% for light vs. dark blue (an Elo-score  
352 difference of 38).

353



354

355

356

357

358

359

360

361

362

363

364

365

366

367

368

Figure 3: Establishment of a colour convention. A: evolution of proposers' score with the number of blocks per individual (grey) and on average (in black, error bars represent standard error of the mean). B: Evolution of Elo-score between colours based on proposers' behaviour (the seven colours presented are an approximate match to the colours seen by the baboons). C: change in score for the responders with the change in partition, from transparent to opaque. D: Average responder score for every combination of colour pair depending on the colour pair difference in Elo-score for three performance groups (Low, Medium and High performance). The fitted curve and standard errors are based on a quasibinomial fit.

The maintenance of the colour hierarchy can be achieved through two non-exclusive processes, the responder could watch the choice of the proposer and respond accordingly, or the responder could have learned the hierarchy and respond without watching. To tease apart these two explanations, we introduced an opaque partition between the two participants. We found that the responder's score decreased for 13/15 individuals (Binomial test,  $p = 0.004$ ), but that the

369 average score remained high (Fig. 4C). Most of the decisions taken by the responders are therefore  
370 based on the knowledge of the hierarchy and do not require visual access. However, we noticed  
371 that all the monkeys with very high score with the transparent partition (above 85%) suffered from  
372 the introduction of the opaque partition, suggesting these individuals watched the proposer. To test  
373 this hypothesis, we divided the group of 19 individuals into three equally sized groups with Low,  
374 Medium and High performing individuals during the transparent condition. For each group we  
375 pooled the data and calculated the average score for every pair of colours. Since these data are  
376 non-independent (the same colour appears in multiple pairs), we used a non-parametric correlation  
377 test to evaluate the relationship between the average score of every pair of colours with the  
378 difference in Elo-score depending on the transparent and opaque conditions (Fig.4D). We found  
379 that high performing monkeys used their knowledge of the hierarchy of colours when the Elo-score  
380 difference between the stimuli was high and resorted to visual checking of their social partner when  
381 the difference was small (Kendall,  $N = 5$ ,  $\tau = -0.42$ ,  $z = -2.66$ ,  $p = 0.008$ ). In contrast, medium or low  
382 performing individuals seem to have only learned the dominance hierarchy of colours, and  
383 therefore have a lower score when the rank difference is small (Medium: Kendall,  $N = 5$ ,  $\tau = -0.13$ ,  $z$   
384  $= -0.85$ ,  $p = 0.40$ ; Low: Kendall,  $N = 5$ ,  $\tau = -0.06$ ,  $z = -0.36$ ,  $p = 0.72$ ).

385         The results of study 1 therefore show that when baboons had to coordinate by choosing the  
386 same colour among a pair, they quickly created a hierarchy between colours that improved their  
387 performance (the score increased). All the monkeys that participated regularly learned at least part  
388 of the hierarchy. In addition, some monkeys also watched their partner to respond appropriately  
389 when the pairs were difficult to discriminate. The hierarchical organisation of colours, although  
390 stable, does not seem to be arbitrary because the score at the beginning of the experiment was  
391 already initially high, suggesting that baboons did not choose colours arbitrarily but based on pre-  
392 existing preferences. To test the generality of our results, the arbitrariness and stability of  
393 conventions we conducted two additional sets of experiments.

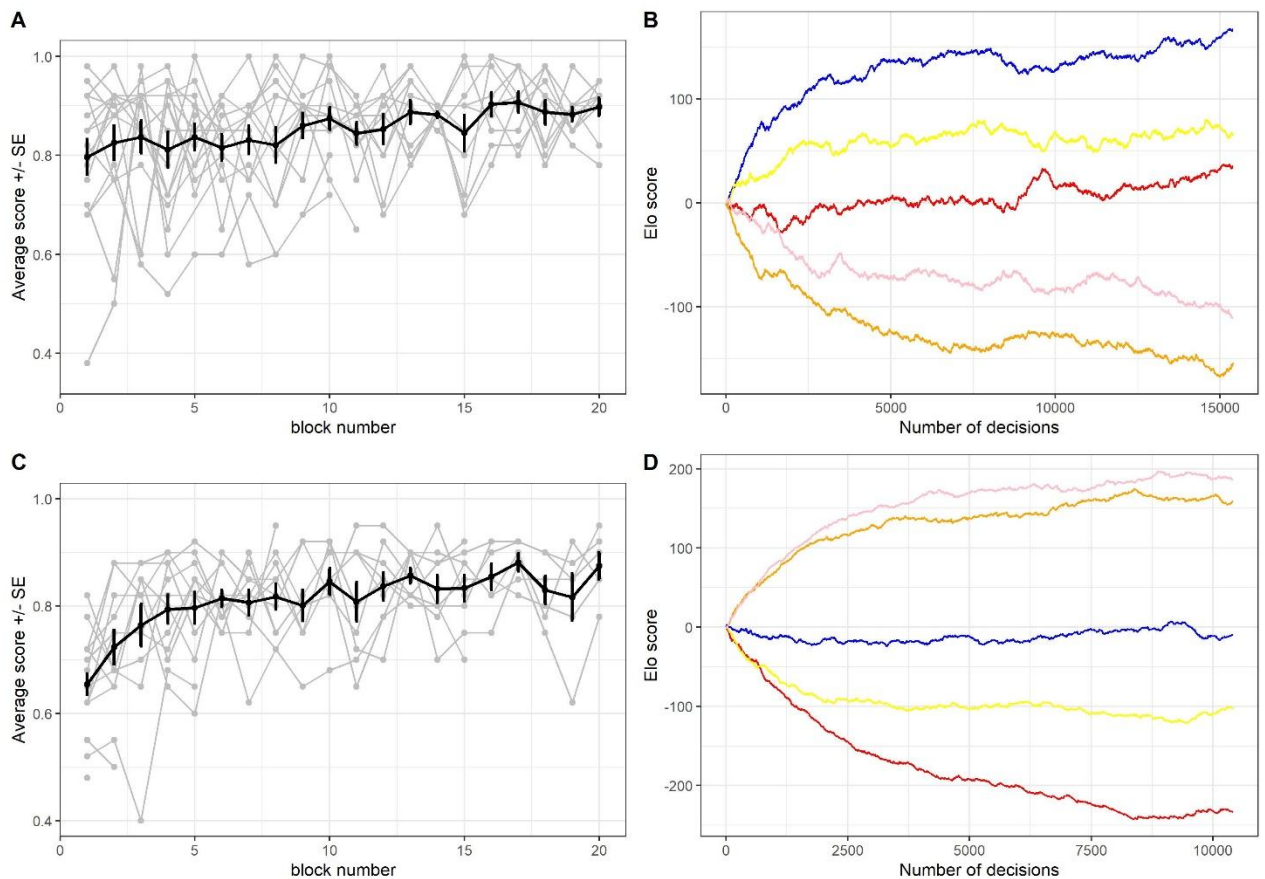
394

395

## 6. Study 2: generalisation of the results

396 We replicated the results of study 1 with a new set of five black and white images to test the  
397 generality of our conclusions (Fig.4, experiment 2.1; see video 2 in ESM). We found equivalent  
398 results to our first study, the score of the proposers increased in a similar fashion ( $\beta = 0.02$ , 95%CI =  
399 [0.01,0.04]) and was linked to the dominance hierarchy that emerged during the experiment  
400 (Kendall,  $N = 10$ ,  $\tau = 0.91$ ,  $z = 3.67$ ,  $p < 0.001$ ). Although the deleterious effect of the opaque  
401 partition was less widespread than previously (the responder's score decreased for 11/16  
402 individuals, Binomial test,  $p = 0.11$ ), we found a similar relationship between the monkeys'  
403 performance in the transparent condition and the effect of the opaque partition. The performance  
404 of high performing monkeys decreased more with the introduction of the opaque partition when  
405 the pairs of stimuli were close in Elo-scores than when they were far apart (High performance:  
406 Kendall,  $N = 5$ ,  $\tau = -0.56$ ,  $z = -2.24$ ,  $p = 0.025$ ; Medium: Kendall,  $N = 5$ ,  $\tau = -0.28$ ,  $z = -1.16$ ,  $p = 0.24$ ;  
407 Low: Kendall,  $N = 6$ ,  $\tau = 0.33$ ,  $z = 1.34$ ,  $p = 0.18$ ).

408



409

410

Figure 4: Establishment of conventions with black and white stimuli (top row) and with an

411 opaque partition (bottom row). The first row shows that conventions can be obtained with new

412 stimulus (black and white images) and the second row shows that they can also be obtained

413 without visual contact between the participants (opaque partition). A and C, evolution of score. B

414 and D evolution of hierarchy. Legend is the same as in Fig.1 with the only difference that colours

415 have been arbitrarily attributed to the black and white stimuli.

416

417 Monkeys could therefore establish a convention with different types of stimuli such as coloured

418 squares, or black and white images. Next, in experiment 2.2, we questioned the importance of the

419 transparent condition to establish the convention. Originally, we thought the monkeys would use

420 the opportunity to see the action of their neighbour to choose the correct response, but the results

421 showed that for a majority the introduction of the opaque partition had limited effect or no effect

422 at all. We decided to question the necessity of having visual access to establish a convention by

423 introducing five new black and white stimuli and performing the same experiment but with an

424 opaque partition from the start. Visual inspection of figure 4 did not reveal qualitative differences  
425 between the experiment with a transparent or an opaque partition (Fig.4 and ESM). We noticed  
426 that the average score was lower and the evolution of the dominance less noisy in the opaque  
427 condition, this is consistent with the fact that monkeys sometime rely on visual access, but it could  
428 also be due to differences in the stimuli we presented since we used different stimuli for the two  
429 experiments. Nonetheless, it appeared that individuals could rapidly establish a convention with or  
430 without visual access to their partner's responses.

431






## 432 **7. Study 3: Arbitrariness of convention**

433 A distinctive feature of conventions is their arbitrariness. In experiment 3.1, we tested the  
434 possibility of establishing an arbitrary convention by individually training the same monkeys as in  
435 experiment one and two to choose the five black and white stimuli of experiment 2.1 in the  
436 opposite order of dominance (we used an opaque partition so that monkeys had no visual access to  
437 their neighbours' behaviour; see video 3 and additional details can be found in the ESM). For  
438 instance, in experiment 2.1 we found that the "dog paw" was more dominant than the "leaf", we  
439 therefore trained the monkeys on the opposite choice by rewarding the "leaf" and not the "paw".  
440 This is a strong test of arbitrariness because presumably monkeys ordered the pairs according to  
441 their shared preference, therefore, if an opposite convention is established and remain stable, this  
442 shows that opposite conventions can be maintained (a less stringent test would simply try to  
443 inverse two stimuli for instance).

444 All individuals were trained in the same reversed order. During training, we found, as  
445 expected, that the score was initially very low (for the first two blocks of trial, mean = 0.30, SE =  
446 0.02, min = 0.19, max = 0.43). However, the performance rapidly improved as the monkeys learned  
447 to choose the correct stimuli for each pair (for the last two blocks of each individual, mean score =  
448 0.72, SE = 0.05, min = 0.28, max = 0.99; see also Fig.S19). After the training phase we performed the

449 same coordination experiment with the transparent partition as previously and found that the score  
450 remained high and showed no sign of decreasing ( $\beta = 0.03$ , 95%CI = [-0.03,0.08]). The hierarchy was  
451 also stable (Fig.S20) and in the opposite order of the one previously established (Table 1). This  
452 shows that the established conventions are to some extent arbitrary.

453

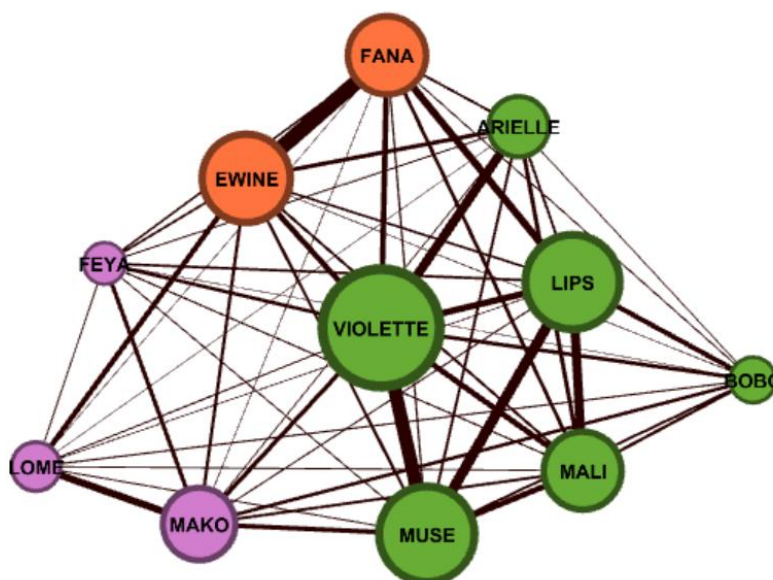
	First exposition	After reversed training
	140	-258
	63	-93
	8	13
	-77	112
	-133	225

454

455 Table 1: Inversion of hierarchy between stimuli after training. First exposition refers to the  
456 spontaneous Elo-scores obtained during experiment 2.1 and “after reversed training” to the Elo-  
457 scores obtained after each individual had been trained on the reversed order.

458 Finally, in experiment 3.2, we wanted to test the impact that each baboon could have on the  
459 establishment of convention based on their social relationships with others. We reasoned that well-  
460 connected individuals could either be influential and change others or, on the contrary, be more  
461 flexible and adapt to others. We selected 11 individuals that had taken part in previous experiments  
462 and used data from experiment 2.1 (generalisation of the results, transparent condition, N= 38409)  
463 to calculate the number of times two individuals performed trials together. Using the modularity  
464 classes algorithm available in the software Gephi, we identified three clusters (Fig. 5). From each  
465 cluster, we selected the individual with the highest degree (Mako, Violette, Ewine) and individually

466 trained them on five new stimuli organised in an arbitrary hierarchy. The remaining eight individuals  
467 were trained using the same procedure but in the reverse order (Fig.6 and ESM for details on  
468 training). Once trained, we tested the establishment of a new convention with a transparent  
469 partition as before.

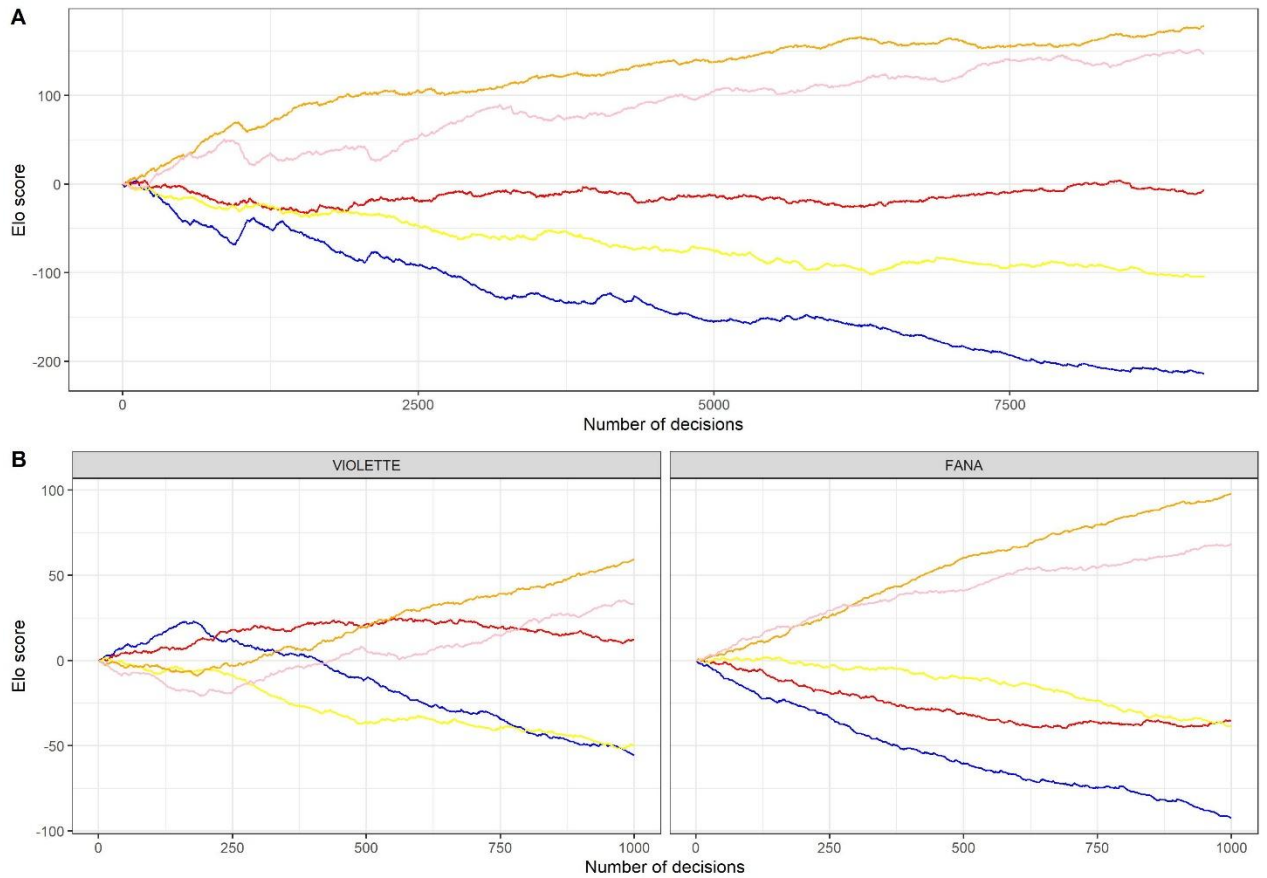


470  
471 Figure 5: Social network of the 11 individuals tested in experiment 3.2. Individuals with  
472 highest degree in their cluster (Mako, Violette, Ewine) were trained on the opposite convention  
473 compared to other individuals. The social network was obtained using the Force Atlas algorithm of  
474 Gephi (Bastian, Heymann, & Jacomy, 2009). Colours indicate different clusters, determined using  
475 Modularity classes. The thickness of the links represents the weight of the links between two  
476 individuals (equivalent to their number of trials performed together). The size of the nodes  
477 represents the weighted degree of the node (i.e. the sum of the link weights).

478  
479 Individuals rapidly learned to choose the correct stimuli during training (for the last two  
480 blocks of each individual, mean score = 0.86, SE = 0.03, min = 0.66, max = 0.96; see also Fig.S24 for  
481 the evolution through time). During the coordination experiment, we found that the group  
482 converged on the convention of the low-degree individuals (Fig.6A) because high-degree individuals  
483 changed their behaviour more than did low-degree individuals. For instance, as can be seen on



484 Fig.6B, the most dominant and least dominant stimuli were reversed for Violette (High degree) and  
485 did not change for Fana (Low degree; see Fig.S27 for the plots of each individual).



486  
487 Figure 6: Evolution of Elo-scores trajectories for the entire group (A) and for the first 1000  
488 trials of two individuals (B), Violette (high degree group) and Fana (low degree group).

489

## 490 8. Discussion and conclusions

491 In this series of experiments, we showed that when monkeys were faced with a coordination  
492 problem, they could spontaneously develop efficient arbitrary stable conventions. Conventions  
493 were efficient because the score improved with the emergence of conventions and because we  
494 found a direct relationship between the score and the hierarchy among the stimuli (Study 1 and  
495 2.1). We showed that conventions were arbitrary and stable because after training to choose stimuli  
496 according to a new hierarchy, monkeys could establish and maintain a new convention based on  
497 this new hierarchy (Study 3.1). These three properties are defining features of human conventions

498 and our results therefore complement a small number of field studies (discussed previously)  
499 showing that non-human primates and maybe other animals can establish conventions akin to  
500 humans.

501 Our results also speak more generally to our understanding of conventions and how they are  
502 established. Moore (2013) for instance raises two important questions in the context of linguistic  
503 conventions: (1) which manner of learning would allow the acquisition of convention? And what  
504 must we know in order to participate in convention? Further specifying that:

505 "Where a coordinating tool acquires its functional properties through convention, those who  
506 learn it must be particularly attentive to the nature of the action that others perform—that  
507 is, to the means R that an observed agent employs in pursuit of her goal E. That's because in  
508 conventional coordination, unlike in the case of nut-cracking described at the outset, one  
509 couldn't (unless one was very lucky) figure out the appropriate means to a goal  
510 independently of copying the actions performed by others." (Moore, 2013; R stands for  
511 regularity in behaviour and E for end goal)

512 In our study, monkeys established a new convention without any visual access to each other's  
513 behaviour (experiment 2.2), therefore showing that imitation, or more generally observational  
514 learning, is not necessary to establish conventions: in the opaque condition baboons were able to  
515 establish a convention through positive reinforcement and knew nothing about the behaviour of  
516 their conspecifics. However, we also found that the most successful monkeys were able to copy the  
517 proposer when the task became difficult due to a small Elo-score difference between pairs of stimuli  
518 (Fig.3D: when the difference in elo-score is small the effect of the opaque partition on the score of  
519 high performing monkeys is stronger). This is in agreement with the growing literature on social  
520 learning showing that individuals can learn from the observation of conspecifics (Whiten, 2021) and  
521 with another study showing this effect with touch-screen (Subiaul, Cantlon, Holloway, & Terrace,  
522 2004).

523           According to Lewis (1969), there are three main sources explaining the emergence of  
524 conventions: *agreement*, *saliency* and *precedence*. Agreement occurs when individuals can  
525 communicate and form mutual expectations (i.e. agree on a course of action), for instance when  
526 making an appointment. Conventions can also emerge when a solution is so salient that most  
527 individuals tend towards that solution (i.e a preference system). Finally, conventions can emerge  
528 through precedence: if a solution becomes more salient and remarkable because it was previously  
529 successfully chosen (i.e. a regularity of behaviour). In the context of our study, agreement is unlikely  
530 to explain the emergence of conventions because monkeys (1) cannot explicitly agree on which  
531 colour to choose and moreover (2) continued to follow convention when the opaque partition  
532 prevented observation of their partner. On the other hand, monkeys can create conventions  
533 through a combination of saliency and precedence. Monkeys may all perceive certain stimuli as  
534 more salient than others (*saliency*) and the result of each trial also influences the stimuli future  
535 saliency (*precedence*).

536           In humans, studies have described tipping points and the role of a determined minority in  
537 changing an established convention (Andreoni, Nikiforakis, & Siegenthaler, 2021; Centola, Becker,  
538 Brackbill, & Baronchelli, 2018). We attempted to study the importance of well-connected  
539 individuals (with a high degree within their cluster), reasoning that if well-connected individuals  
540 were to change their behaviour this could change the whole group. Contrary to our expectations we  
541 found that well-connected individuals were more likely to adapt to others rather than influence  
542 them. Given that high-degree individuals were also a minority (three vs. eight), several factors could  
543 explain this result. Individuals may have been conformist and followed the majority for instance  
544 (e.g. Haun, Rekers, & Tomasello, 2012), or they may be well-connected *because* they are flexibly  
545 adapting to others. Additional experiments will be able to provide a more detailed understanding of  
546 the influence of network parameters and other biases by manipulating the proportion and identity  
547 of individuals that are trained on alternative conventions.

548 Conventions are an important aspect of human culture because like norms they stabilise  
549 cultural diversity. Surprisingly, although the evolutionary precursors of conventions and norms exist  
550 in non-human primates(Kappeler et al., 2019), conventions do not seem to be widespread and their  
551 contribution to non-human primate culture seems almost anecdotal. One might therefore be  
552 tempted to think that conventions require elaborate social learning mechanisms. Using a freely  
553 accessible touch-screen system in which pairs of individuals can perform experiments together, we  
554 have shown, through five experiments, that non-human primates can develop conventions using  
555 positive reinforcement learning and that although copying can be used by some individuals, it is not  
556 necessary.

### 557 **Acknowledgments**

558 We thank Julie Gullstrand and Sebastien Barniaud as well as the staff at the Rousset-sur-Arc  
559 Primate Center (CNRS-UPS846, France) for technical supports.

### 560 **Ethics**

561 This research was carried out in accordance with European Union and French ethical  
562 standards and received approval from the French Ministère de l'Éducation Nationale et de la  
563 Recherche (approval no. APAFIS-2717-2015111708173794-V3).

### 564 **Data Accessibility**

565 The data and analysis code used in this article are available here:

566 <https://osf.io/b68x2/>

### 567 **Authors' Contributions**

568 A.F., N.C., J.F. planned the experiment, D.P., N.C., J.F. planned and constructed the S-ALDMs,  
569 A.F., N.C. performed the experiment, A.F., N.C. analysed the results, A.F., N.C., J.F. wrote the  
570 manuscript.

### 571 **Competing Interests**

572 We have no competing interests.

### 573 **Funding**

574 This project received funding from the Institute for Language Communication and the Brain  
575 (ILCB) through the Agence Nationale de la Recherche grant ANR-16-CONV-0002

## 576 **9. References**

- 577 Andreoni, J., Nikiforakis, N., & Siegenthaler, S. (2021). Predicting social tipping and norm change in  
578 controlled experiments. *Proceedings of the National Academy of Sciences*, *118*(16),  
579 e2014893118. doi:[10.1073/pnas.2014893118](https://doi.org/10.1073/pnas.2014893118)
- 580 Arnold, K., & Zuberbühler, K. (2008). Meaningful call combinations in a non-human primate. *Current*  
581 *Biology*, *18*(5), R202-R203. doi:<https://doi.org/10.1016/j.cub.2008.01.040>
- 582 Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random  
583 effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390-412.  
584 doi:<http://dx.doi.org/10.1016/j.jml.2007.12.005>
- 585 Bastian, M., Heymann, S., & Jacomy, M. (2009). *Gephi: an open source software for exploring and*  
586 *manipulating networks*. Paper presented at the International AAAI Conference on Weblogs  
587 and Social Media, San Jose, California, USA.
- 588 Berg, E. A. (1948). A Simple Objective Technique for Measuring Flexibility in Thinking. *The Journal of*  
589 *General Psychology*, *39*(1), 15-22. doi:10.1080/00221309.1948.9918159
- 590 Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical Classification by  
591 Rank and Kinship in Baboons. *Science*, *302*(5648), 1234-1236. doi:10.1126/science.1087513
- 592 Bicchieri, C. (2005). *The grammar of society: The nature and dynamics of social norms*: Cambridge  
593 University Press.
- 594 Bickerton, D. (1981). *Roots of language*. Ann Arbor: Karoma Publishers.
- 595 Bonté, E., Flemming, T., & Fagot, J. (2011). Executive control of perceptual features and abstract  
596 relations by baboons (*Papio papio*). *Behavioural Brain Research*, *222*(1), 176-182.  
597 doi:<https://doi.org/10.1016/j.bbr.2011.03.034>

598 Centola, D., Becker, J., Brackbill, D., & Baronchelli, A. (2018). Experimental evidence for tipping  
599 points in social convention. *Science*, 360(6393), 1116. doi:10.1126/science.aas8827

600 Deming, W., Neumann, J., & Morgenstern, O. (1944). Theory of Games and Economic Behavior.  
601 *Journal of the American Statistical Association*, 40, 263.

602 Elo, A. E. (1978). *The rating of chessplayers, past and present*: Arco Pub.

603 Fagot, J., Gullstrand, J., Kemp, C., Defilles, C., & Mekaouche, M. (2014). Effects of freely accessible  
604 computerized test systems on the spontaneous behaviors and stress level of Guinea  
605 baboons (*Papio papio*). *American Journal of Primatology*, 76(1), 56-64.  
606 doi:10.1002/ajp.22193

607 Fagot, J., Marzouki, Y., Huguet, P., Gullstrand, J., & Claidière, N. (2015). Assessment of Social  
608 Cognition in Non-human Primates Using a Network of Computerized Automated Learning  
609 Device (ALDM) Test Systems. *JoVE*(99), e52798. doi:doi:10.3791/52798

610 Fay, N., Garrod, S., Roberts, L., & Swoboda, N. (2010). The Interactive Evolution of Human  
611 Communication Systems. *Cognitive Science*, 34(3), 351-386.  
612 doi:<https://doi.org/10.1111/j.1551-6709.2009.01090.x>

613 Fedigan, L. (1993). Sex differences and intersexual relations in adult white-faced capuchins (*Cebus*  
614 *capucinus*). *International Journal of Primatology*, 14(6), 853-877. doi:10.1007/BF02220256

615 Fudenberg, D., & Maskin, E. (2008). THE FOLK THEOREM IN REPEATED GAMES WITH DISCOUNTING  
616 OR WITH INCOMPLETE INFORMATION. In *A Long-Run Collaboration on Long-Run Games* (pp.  
617 209-230): WORLD SCIENTIFIC.

618 Galantucci, B. (2005). An Experimental Study of the Emergence of Human Communication Systems.  
619 *Cognitive Science*, 29(5), 737-767. doi:[https://doi.org/10.1207/s15516709cog0000\\_34](https://doi.org/10.1207/s15516709cog0000_34)

620 Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E.  
621 (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology*  
622 *and Sociobiology*, 67(3), 373-381. doi:10.1007/s00265-012-1457-6

623 Goodrich, B., Gabry, J., Ali, I., & Brilleman, S. (2020). rstanarm: Bayesian applied regression  
624 modeling via Stan (Version 2.21.1). Retrieved from <https://mc-stan.org/rstanarm>

625 Graham, K. E., Hobaiter, C., Ounsley, J., Furuichi, T., & Byrne, R. W. (2018). Bonobo and chimpanzee  
626 gestures overlap extensively in meaning. *PLOS Biology*, 16(2), e2004825.  
627 doi:10.1371/journal.pbio.2004825

628 Haun, D. B. M., Rekers, Y., & Tomasello, M. (2012). Majority-Biased Transmission in Chimpanzees  
629 and Human Children, but Not Orangutans. *Current biology*, 22(8), 727-731. Retrieved from  
630 <http://linkinghub.elsevier.com/retrieve/pii/S0960982212002631>

631 Hawkins, R. X. D., & Goldstone, R. L. (2016). The Formation of Social Conventions in Real-Time  
632 Environments. *PLoS ONE*, 11(3), e0151670. doi:10.1371/journal.pone.0151670

633 Hawkins, R. X. D., Goodman, N. D., & Goldstone, R. L. (2019). The Emergence of Social Norms and  
634 Conventions. *Trends in Cognitive Sciences*, 23(2), 158-169.  
635 doi:<https://doi.org/10.1016/j.tics.2018.11.003>

636 Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews*,  
637 69(2), 207-231. doi:10.1111/j.1469-185X.1994.tb01506.x

638 Hume, D. (1888). *A treatise of human nature*: Oxford Univ Press.

639 Kappeler, P. M., Fichtel, C., & van Schaik, C. P. (2019). There Ought to Be Roots: Evolutionary  
640 Precursors of Social Norms and Conventions in Non-Human Primates. In *The Normative*  
641 *Animal?* New York: Oxford University Press.

642 Kegl, J. (1994). The Nicaraguan sign language project: An overview. *Signpost*, 7, 24-31.

643 Kemp, C., Rey, A., Legou, T., Boë, L.-J., Berthommier, F., Becker, Y., & Fagot, J. (2017). Vocal  
644 Repertoire of Captive Guinea Baboons (*Papio papio*). *Origins of Human Language: Continuities and Discontinuities with Nonhuman Primates*, 15.

645

646 Laidre, M. E. (2011). Meaningful Gesture in Monkeys? Investigating whether Mandrills Create Social  
647 Culture. *PLoS ONE*, 6(2), e14610. Retrieved from  
648 <http://dx.doi.org/10.1371/journal.pone.0014610>

649 Lewis, D. (1969). *Convention: A philosophical study*: Harvard Univ Pr.

650 McGrew, W. C., Marchant, L. F., Scott, S. E., & Tutin, C. E. G. (2001). Intergroup Differences in a  
651 Social Custom of Wild Chimpanzees: The Grooming Hand Clasp of the Mahale Mountains.  
652 *Current Anthropology*, 42(1), 148-153. Retrieved from  
653 <http://www.journals.uchicago.edu/doi/abs/10.1086/318441>

654 Moore, R. (2013). Imitation and conventional communication. *Biology & Philosophy*, 28(3), 481-500.  
655 doi:10.1007/s10539-012-9349-8

656 Muth, C., Oravecz, Z., & Gabry, J. (2018). User-friendly Bayesian regression modeling: A tutorial with  
657 rstanarm and shinystan. *Quantitative Methods for Psychology*, 14(2), 99-119.

658 Nakamura, M., McGrew, W. C., Marchant, L. F., & Nishida, T. (2000). Social scratch: Another custom  
659 in wild chimpanzees? *Primates*, 41(3), 237-248. doi:10.1007/BF02557594

660 Nash, J. (1951). Non-cooperative games. *Annals of mathematics*, 286-295.

661 Nichols, S. (2002). On The Genealogy Of Norms: A Case For The Role Of Emotion In Cultural  
662 Evolution. *Philosophy of Science*, 69(2), 234-255. doi:doi:10.1086/341051

663 Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's Monkeys Use Affixation to Alter  
664 Call Meaning. *PLoS ONE*, 4(11), e7808. doi:10.1371/journal.pone.0007808

665 Perry, S., Baker, M., Fedigan, L., Grosa Louis, J., Jack, K., MacKinnon, Katherine C., . . . Rose, L.  
666 (2003). Social conventions in wild white faced Capuchin monkeys: Evidence for traditions in  
667 a neotropical primate. *Current Anthropology*, 44(2), 241-268. doi:10.1086/345825

668 R Core Team. (2021). R: A language and environment for statistical computing. Vienna, Austria: R  
669 Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>.

670 Sánchez-Tójar, A., Schroeder, J., & Farine, D. R. (2018). A practical guide for inferring reliable  
671 dominance hierarchies and estimating their uncertainty. *Journal of Animal Ecology*, 87(3),  
672 594-608. doi:<https://doi.org/10.1111/1365-2656.12776>

673 Sapolsky, Robert M. (2006). Social Cultures among Nonhuman Primates. *Current Anthropology*,  
674 47(4), 641-656. doi:10.1086/504162



675 Sapolsky, R. M., & Share, L. J. (2004). A pacific culture among wild baboons: Its emergence and  
676 transmission. *PLoS Biology*, 2(4), 534-541. Retrieved from <Go to ISI>://000221194700020

677 Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social Bonds Enhance Reproductive  
678 Success in Male Macaques. *Current Biology*, 20(24), 2207-2210.  
679 doi:<https://doi.org/10.1016/j.cub.2010.10.058>

680 Silk, J. B. (2007). Social Components of Fitness in Primate Groups. *Science*, 317(5843), 1347-1351.  
681 doi:10.1126/science.1140734

682 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . . Cheney, D. L.  
683 (2009). The benefits of social capital: close social bonds among female baboons enhance  
684 offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, 276(1670), 3099-  
685 3104. doi:10.1098/rspb.2009.0681

686 Slater, P. J. B. (1986). The cultural transmission of bird song. *Trends in Ecology & Evolution*, 1(4), 94-  
687 97. doi:[https://doi.org/10.1016/0169-5347\(86\)90032-7](https://doi.org/10.1016/0169-5347(86)90032-7)

688 Snowdon, C. T., & Elowson, A. M. (1999). Pygmy Marmosets Modify Call Structure When Paired.  
689 *Ethology*, 105(10), 893-908. doi:<https://doi.org/10.1046/j.1439-0310.1999.00483.x>

690 Stephens, D. W., & Heinen, V. K. (2018). Modeling nonhuman conventions: the behavioral ecology  
691 of arbitrary action. *Behavioral Ecology*, 29(3), 598-608. doi:10.1093/beheco/ary011

692 Strauss, E. D., & Holekamp, K. E. (2019). Inferring longitudinal hierarchies: Framework and methods  
693 for studying the dynamics of dominance. *Journal of Animal Ecology*, 88(4), 521-536.  
694 doi:<https://doi.org/10.1111/1365-2656.12951>

695 Subiaul, F., Cantlon, J. F., Holloway, R. L., & Terrace, H. S. (2004). Cognitive Imitation in Rhesus  
696 Macaques. *Science*, 305(5682), 407-410. doi:10.1126/science.1099136

697 Tomasello, M. (2008). *Origins of human communication*: MIT press.

698 Tomasello, M., & Call, J. (1997). *Primate cognition*: Oxford University Press.

