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The experimental emergence of convention in a non-human primate

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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 group¹.
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

¹ 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**

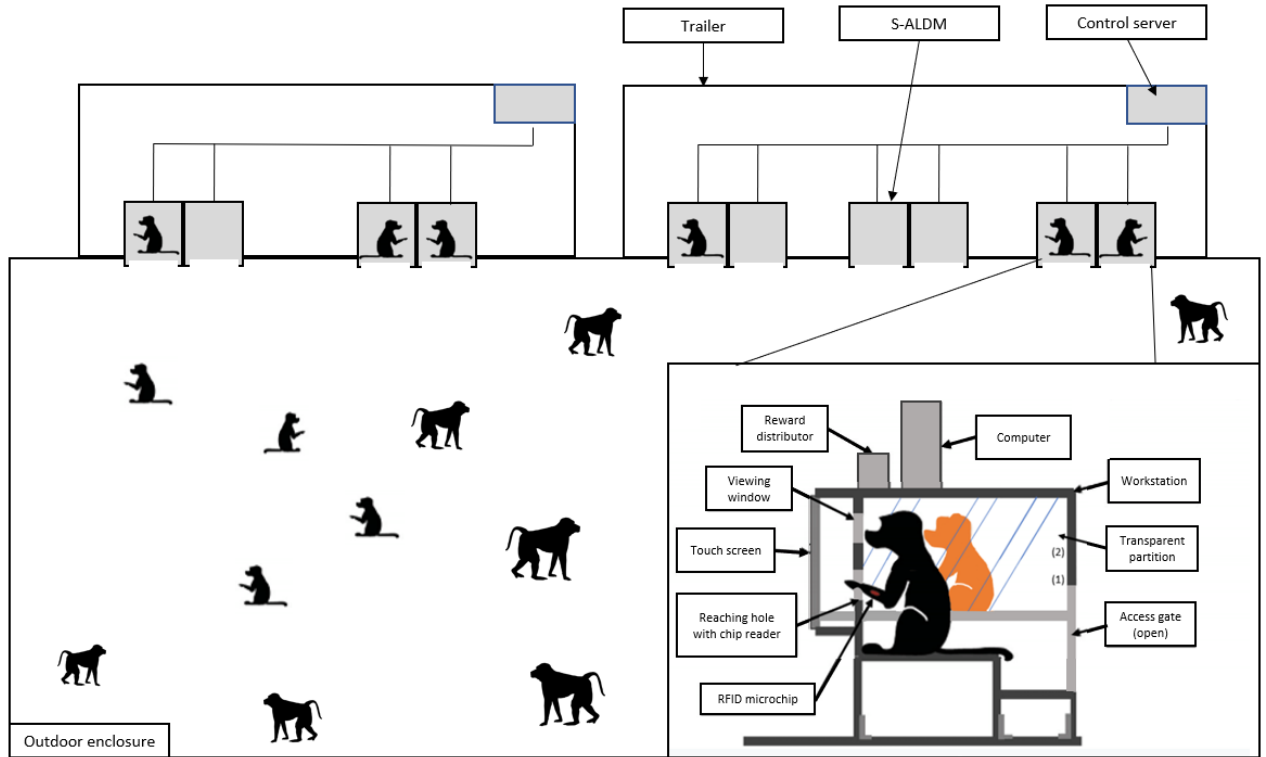
238 **Section 4.1 Participants**

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.



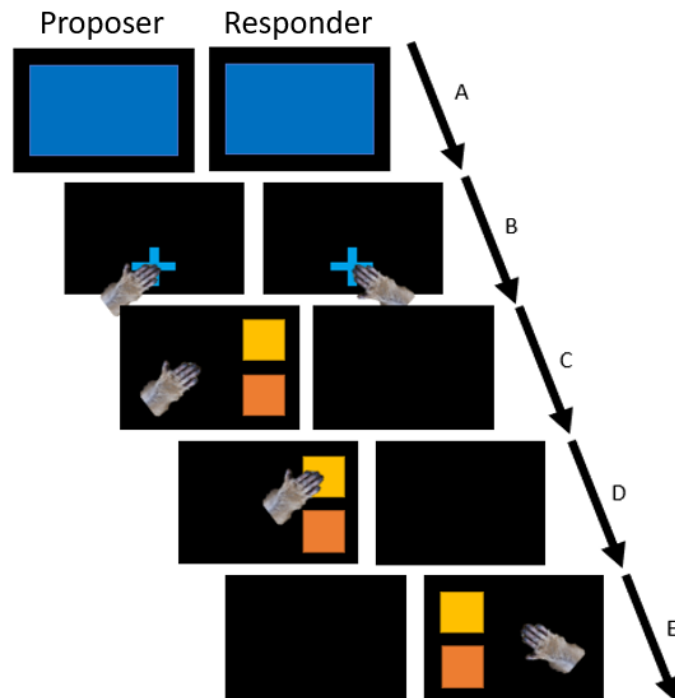
259
 260 Figure 1: (a) 19 baboons living in an enclosure have *ad libitum* access to two trailers, each
 261 containing several S-ALDMs. The diagram shows the two bungalows and the five units. (b) Detail of
 262 the organization of a workstation, where two monkeys can work side by side, while seeing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

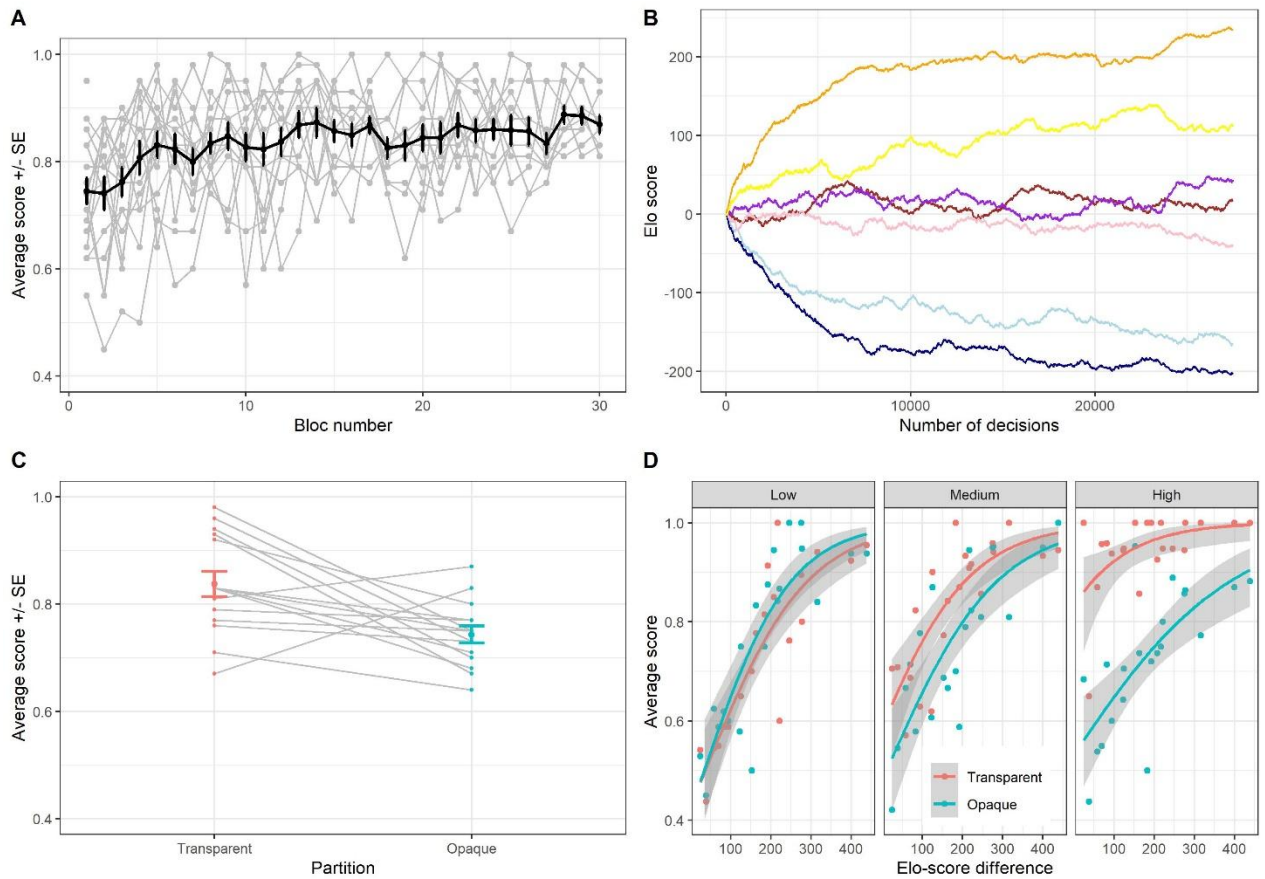
321 We performed several experiments in which we manipulated the partition between
322 individuals (either transparent or opaque) and the stimuli (all stimuli are freely available with the
323 data and code to analyse the results). Since these experiments are based on the voluntary partition
324 of monkeys, 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 (β
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).

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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.

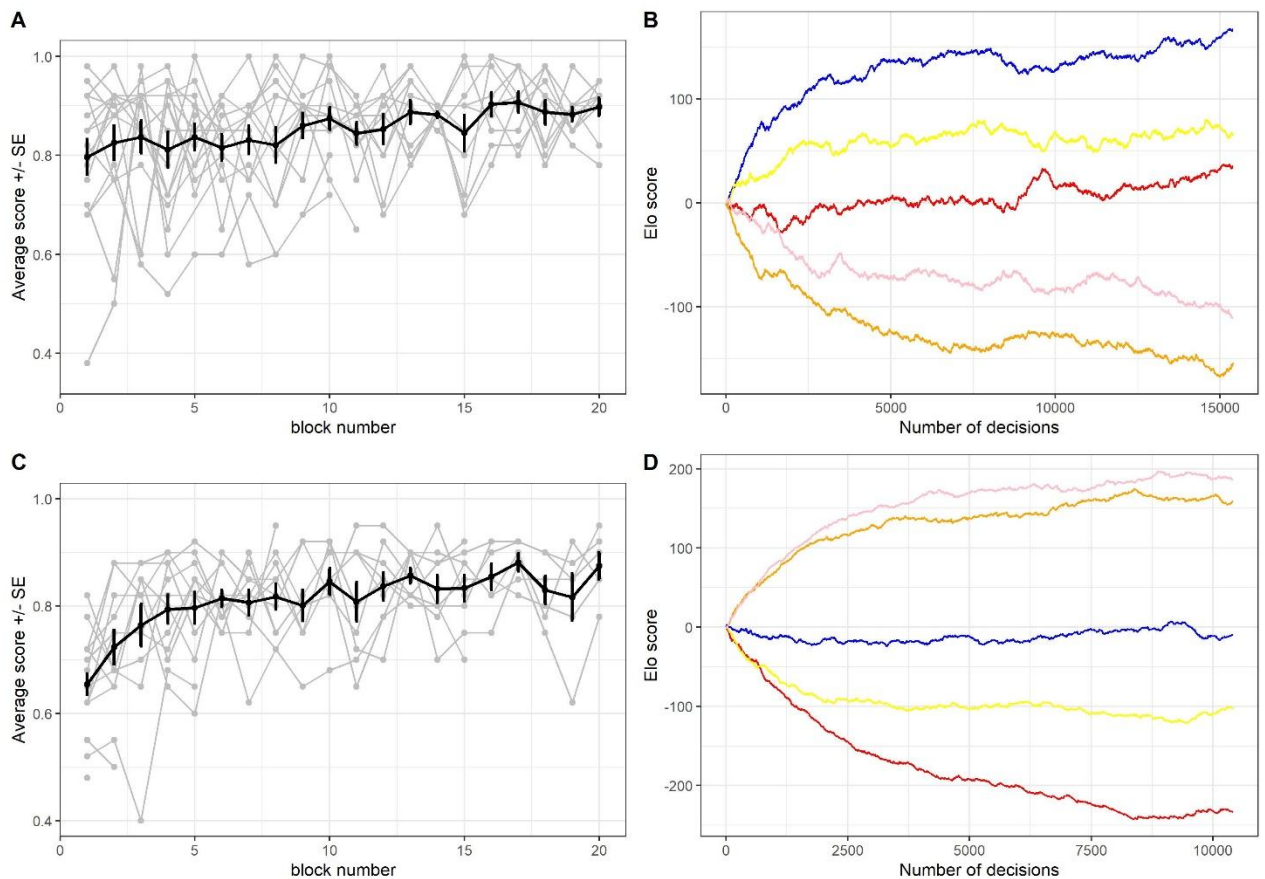
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6. Study 2: generalisation of the results

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, $N = 6$, $\tau = 0.33$, $z = 1.34$, $p = 0.18$).

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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

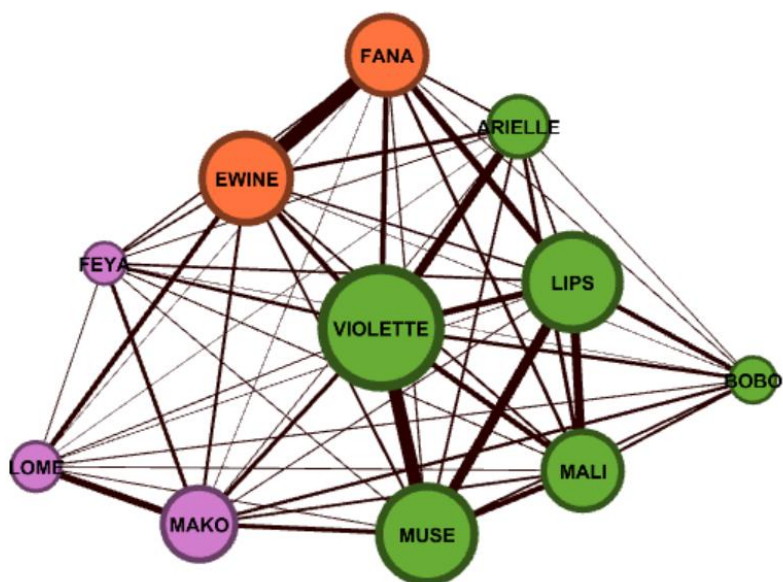
| | First exposition | After reversed training |
|---|------------------|-------------------------|
|  | 140 | -258 |
|  | 63 | -93 |
|  | 8 | 13 |
|  | -77 | 112 |
|  | -133 | 225 |

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

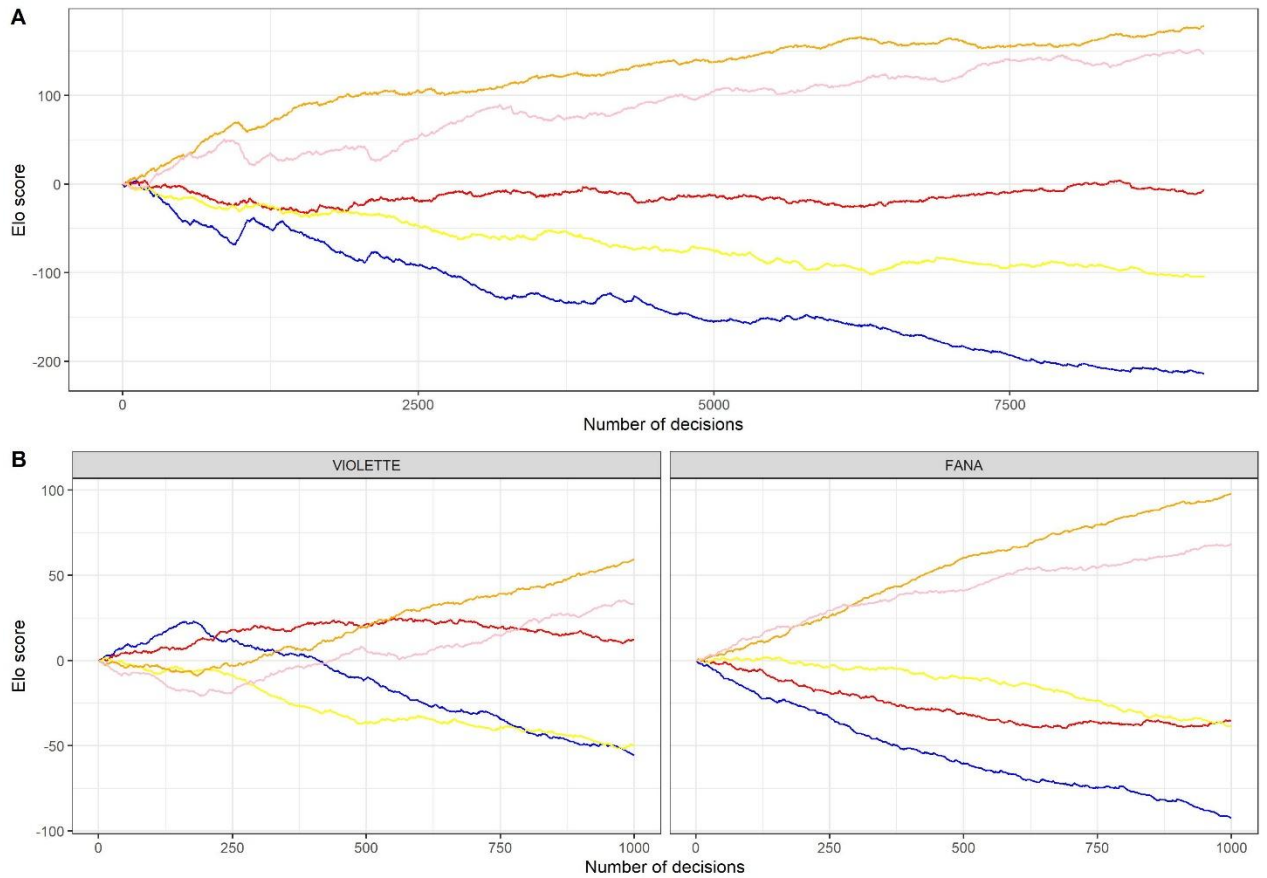
466 trained them on five new stimuli organised in an arbitrary hierarchy. The remaining eight individuals
467 were trained using the same procedure but in the reverse order (Fig.6 and ESM for details on
468 training). Once trained, we tested the establishment of a new convention with a transparent
469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

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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.

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