The experimental emergence of convention in a non-human primate

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Abstract

Conventions form an essential part of human social and cultural behaviour and may also be important to other animals. Yet, despite the wealth of evidence that has accumulated for culture in non-human animals, we know surprisingly little about non-human conventions beyond a few rare examples. We follow the literature in behavioural ecology and evolution and define conventions as behaviours that solve a coordination problem in which two or more individuals need to display complementary behaviour to obtain a mutually beneficial outcome. We review and discuss the literature on conventions in non-human primates and come to the conclusion that all the ingredients for conventions to emerge are present and therefore that they ought to be more frequently observed. We probe emergence of conventions by using a unique novel experimental system in which pairs of baboons (*Papio papio*) can voluntarily participate together in touch-screen based cognitive testing and we show that conventions readily emerge in our experimental setup and that they share three fundamental properties of human conventions (arbitrariness, stability and efficiency). These results question the idea that imitation is necessary to establish conventions.

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

26 **1. Introduction**

27 Conventions form an essential part of human social and cultural behaviour and may also be
28 important to other animals. Yet we know surprisingly little about non-human conventions beyond a
29 few rare examples (see Stephens & Heinen, 2018 for a discussion of non-human conventions). The
30 purpose of this article is to discuss and review the literature on conventions in non-human primates
31 to provide a background against which human conventions have evolved (Kappeler, Fichtel, & van
32 Schaik, 2019) and then to present a succession of experiments showing the emergence of convention
33 in a non-human primate using a unique novel experimental system. These experiments show that
34 baboons (*Papio papio*) can easily develop conventions that share at least three properties of human
35 conventions (arbitrariness, stability and efficiency) through simple reinforcement learning. Before we
36 begin however, we start by clarifying the meaning and properties of convention.

37 Intuitively conventions are rule like behaviour such as “driving on the right side”, “saying
38 ‘hello’ as a greeting” or “eating cheese before dessert”. Beyond this intuitive understanding however,
39 conventions have proven difficult to define and have been much debated. Here, we will follow a
40 ‘Lewisian’ approach (Lewis, 1969) and define conventions as ways to systematically solve a
41 coordination problem. In a coordination problem, two or more individuals benefit from acting
42 together, that is, from considering the behaviour of another individual.

43 A classic example of convention, used by Hume (1888) and taken up by Lewis, is that of two
44 rowers on a boat. If both rows are synchronized, the boat will move forward smoothly, whereas if
45 they row out of sync, it will behave erratically. In Hume's (then Lewis's) use, this example illustrate
46 the main properties of convention: 1) rowers do not keep promises to act in concert, 2) they may
47 express their shared interest explicitly, but not necessarily, 3) to row in rhythm, there must be a
48 gradual installation of synchronous behaviour, 4) they may know that what is being set up between
49 them is a convention, but not know how to describe it verbally ("We start at the 90° angle and give a

stroke every 2 seconds") and 5) they have adopted a rhythm that they keep because it works, but there are alternatives. We discuss some of these characteristics in more detail below.

Individuals can find ad hoc solutions to coordination problems when they arise, as when finding seating arrangements around the table for instance. However, when coordination problems happen regularly and/or impose a high cost for a failure to coordinate, individuals may benefit from establishing a convention (Hawkins & Goldstone, 2016). Notice that compared to other types of positive interactions such as helping (one individual benefits at the expense of another) or cooperation (individuals can benefit more by being selfish), individuals mutually benefit from coordination: it is in their own best interest and in the interest of the partner(s) to coordinate. Therefore, there is no conflict of interest between individuals when solving a coordination problem or when establishing a convention. Rather, conventions are important because they help stabilise interactions by creating mutual expectations between individuals. Someone picking up his/her car in France expects other individuals to drive on the right side of the road and so adjusts his/her behaviour accordingly. These expectations need not be explicit nor mutually acknowledged for a convention to exist (Moore, 2013). In fact, sometimes we are barely aware that a convention exists: you might lunch at a certain time simply because you expect other people to lunch around that time. According to Hawkins' theoretical model (2019), three processes allow the emergence and maintenance of a convention: the population level (social network management and cultural transmission), the dyad level (coordination and social interaction) and the individual level (executive functions and expectations). A convention is not necessarily created as a result of a problem encountered by the whole population at one point. If enough dyads in the population repeatedly encounter a coordination problem and each individual belongs to several dyads, a population-wide convention can emerge.

Conventions are traditionally distinguished from habits and norms. Habits are patterns of individual behaviour that do not (strongly) depend on other individuals, but they can be shared and cultural: taking a shower vs. taking a bath for instance. In contrast, norms may be seen as solving

coordination problems when the interest of individuals are not aligned. They are associated to a sense of “oughtness” and punishment that conventions and habits lack, e.g. “you ought not to cheat” (e.g. Bicchieri, 2005). Clearly, given the diversity of human social behaviour, there are no strict boundaries between habits, conventions, and norms. What was once a habit, “spitting in the street”, can become a norm “do not spit” (Nichols, 2002). Conventions, e.g. “driving on the right side” can be felt to some like norms that ought to be followed at all times and be enforced by punishment. There are also habits, “eating with chopsticks”, that, although not a coordination problem per se, are easier to deal with when everyone follows the same rules (e.g. to dress the table). Therefore, conventions are not an “all or nothing” kind of thing but a “more or less” one: behaviour are more or less conventional depending on how closely they match the prototypical example of convention.

In the framework of game theory (Deming, Neumann, & Morgenstern, 1944), a coordination problem is a problem with multiple Nash equilibria (a strategy is a Nash equilibrium when no player can do better by changing his strategy alone; (Nash, 1951)) and a convention is a stable solution to such problem (see Lewis (1969) for the original discussion and Stephens and Heinen (2018) for a more detailed discussion in the context of animal behaviour). Equilibrium selection, the stable solution that is adopted, is governed by initial conditions and dynamics (influenced by the way individuals choose to act and the environment). Note that conventions require multiple equilibria, but that different equilibria need not be equally rewarding, one may lead to higher rewards for instance (called payoff dominant strategies) and some equilibrium may be more rewarding than others when individuals deviate from the equilibrium (risk dominant equilibrium). Importantly, repetition can help create conventions because with repetition multiple equilibrium often appear (Fudenberg & Maskin, 2008).

To summarise, when individuals regularly face coordination problems, they may develop conventions as solutions to these problems. Conventions are systematic behaviours that are mutually beneficial and provide stable expectations about other individuals. Thus conventions, like norms, help individuals stabilise their social environment and navigate their social world. It is important to note that conventions do not require individuals to do the same action (one could pull while the other

pushes), they can concern as few as two individuals, and they do not necessarily lead to the optimal solution (other more profitable equilibria may exist). Conventions are usually associated with three important properties (Hawkins & Goldstone, 2016):

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

Conventions are the natural outcome of individuals repeatedly facing coordination problems together and are therefore expected in group living animals and especially in tightly bonded non-human primates. In non-human primates studies have shown that social stability has important fitness benefits (Gilby et al., 2013; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk, 2007; Silk Joan et al., 2009) and given that conventions are stable solutions that are mutually beneficial to individuals, we should expect to find them in our closest relatives. Yet, surprisingly, there are very few examples that we know of.

2. Conventions in non-human primates?

Susan Perry et al's description of social conventions in white-faced capuchin monkeys (*Cebus capucinus*) is one of the best description of conventions we have in non-human primates (Perry et al., 2003). Using 13 years of data collection in their field sites in Costa Rica, Perry et al. describe the fashion like emergence of new behaviour, such as *hand-sniffing* (first reported by Fedigan, 1993) in which one individual hold the hand or foot of another over its own face. These behaviours require coordination between pairs of individuals, emerge in some groups and not others and can spread to a large proportion of individuals within the group. They can also stay stable for a long time, in one group hand-sniffing was observed during seven years before disappearing. These behaviours therefore appear to have all the properties of conventions. Similarly, the *hand-clasp* grooming (McGrew (McGrew, Marchant, Scott, & Tutin, 2001; van Leeuwen, Cronin, Haun, Mundry, & Bodamer,

2012) and *social-scratch* grooming of chimpanzees (Nakamura, McGrew, Marchant, & Nishida, 2000) also appear to meet the requirements of conventions: they are stable behaviour that solve coordination problems for which alternative behaviour exist. In addition, the social organization may vary between groups of the same species and some attitudes may be considered conventional under the definition proposed here. For example, van de Waal (2018) showed that neighbouring groups of vervet monkeys differ in the structure of their social networks as well as how they handle conflict. When conflicts arise within a group, alternative behaviours can be adopted to bring back stability, some groups adopt affiliative behaviours (conciliation or reconciliation) while others adopt agonistic behaviours (coalition or redirection). Another similar example is the emergence and transmission of a "pacific culture" within a group of baboons after most of the most aggressive monkeys died (Sapolsky & Share, 2004). The low level of aggression was maintained in the group despite the migration of new individuals and is therefore a stable alternative to other, more aggressive groups.

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

Some social learning experiments however show some level of conventionality. In the studies of van de Waal, Borgeaud, and Whiten (2013) for instance, groups of vervet monkeys (*Chlorocebus aethiops*) learned to eat food of one colour (e.g. pink) and avoid food from another colour (e.g. blue). Once this preference has been learned, results show that monkeys continue to prefer to eat food of only one colour even when they are exposed to edible versions of both colours. Even more surprisingly, monkeys that migrate from one group (e.g. pink) to another group (e.g. blue) may adopt

the behaviour of members of the group against their own previous preference (e.g. they switch from pink to blue). One possible explanation for the vervet monkeys' behaviour is that they need to compete for food to establish their dominance within the group¹. Indeed, dominance hierarchies are examples of conventions, they are stable solutions to coordination problems (to access food and/or reproduction) and provide stable expectations regarding others' behaviour (see Bergman, Beehner, Cheney, & Seyfarth, 2003). In a particular group there certainly are several stable solutions to organise the dominance between individuals, that organisation is therefore conventional to some extent. However, the dominance hierarchy is also typical of a species and constrained by genetic dispositions.

This consideration is also important to determine if non-human primate communication is conventional. Non-human primates' vocalisations and gestures come from a largely fixed repertoire and are not conventional (e.g. Arnold & Zuberbühler, 2008; Kemp et al., 2017; Ouattara, Lemasson, & Zuberbühler, 2009; Tomasello & Zuberbühler, 2002). Some flexible gestural communications can emerge through "ontogenetic ritualisation" (Tomasello & Call, 1997), a process through which an action at the beginning of an action sequence, such as raising an arm before play-hitting another individual, progressively becomes a signal to initiate the action sequence, raising an arm to initiate rough-and-tumble play (Tomasello, 2008). However, ontogenetic ritualisation cannot give rise to conventions because there is a direct link between the sequence of actions to perform and the signal that is used to initiate it, there is therefore no alternative signal through which this could be initiated (Moore, 2013). For instance, in one group of mandrills (*Mandrillus sphinx*) Laidre (2011) described

¹ We thank Kate Arnold (St Andrews University) for pointing this out to us.

172 the emergence of a novel *eye-covering* gesture probably used to signal that the individual was resting.
173 This gesture was unique to this group and had been observed for nearly a decade in the group and
174 never seen elsewhere. Yet there is probably a direct link between the gesture and what it signals, and
175 alternative gestures (say crossing arms for instance) may not be able to signal the same meaning.

176 Of course, the absence of conventions in non-human primates' communication contrasts
177 sharply with human language that is often considered to be a paradigmatic example of convention
178 since the word-meaning association is largely arbitrary (Lewis, 1969). Noteworthily, Tomasello (2008)
179 has proposed that linguistic and other human conventions are learned by imitation and that the lack
180 of a capacity for imitation in non-human primates could explain both their apparent lack of
181 conventions and their lack of language (see also Moore, 2013). The experiments we present below
182 come to question this idea since we observe the emergence of convention in a non-human primate
183 without imitation.

184

3. Method

Participants

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

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

The ALDM (Fagot & Bonté, 2010; Fagot & Paleressompoulle, 2009) are operant conditioning test systems that can be used for testing non-human primates in social setting. ALDMs used an automatic radio frequency identification device (RFID) implanted in each forearm of the monkeys to recognize the individuals. This device makes it possible to test the animals without having to capture and isolate them (additional information of the setup can be found in Fagot, Gullstrand, Kemp, Defilles, & Mekaouche, 2014; Fagot, Marzouki, Huguet, Gullstrand, & Claidière, 2015). The ALDMs presented in Fagot et al., 2015) were modified in 2018 and connected in pairs to allow an individual in one ALDM to both see its partner and its touchscreen of the neighboring ALDM (see Fig.1b). We dubbed this new version of ALDMs the Social-ALDMs or S-ALDMs for short. Two individuals could therefore see each other and their responses on the screen when a transparent partition between the ALDM was used. All the monkeys had previously participated in studies using this ALDM testing system but had never performed the present experiment.

Figure 1: (a) 19 baboons living in an enclosure have ad libitum access to two trailers, each containing several S-ALDMs. The diagram shows the two bungalows and the five units. (b) Detail of the organization of a workstation, where two monkeys (1 and 2) can work side by side, while seeing each other.

Computerised task

We used two different tasks, one when two individuals are present, the “dual task”, and one when an individual is alone, the “filler task”. These two tasks are presented below. When a monkey entered an ALDM, a blue screen was displayed with a 4-second delay. If another individual was detected in the neighboring ALDM during this delay, a blue screen was also displayed, announcing the synchronization of the two machines and the start of the dual task (Fig.2). Otherwise, if the neighboring ALDM stayed empty for 4 secs, the filler task started. The function of the filler task was mainly to keep the baboons occupied within the S-ALDM while waiting for another individual to arrive.

Dual task

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

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

miss. The success of a test was coded as a binary variable: correct response = 1 and incorrect response = 0. A success triggered the delivery of a reward to the two individuals of the pair, a miss resulted in a 3 secs timeout for both.

Filler task

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

Statistical analysis

The evolution of Score during the experiment was evaluated using a generalized mixed linear model (GLMM, Baayen, Davidson, & Bates, 2008) with binomial error distribution and a logit link function. Models were analysed using the `stan_glmer` function of R's `rstanarm` package (Goodrich, Gabry, Ali, & Brilleman, 2020) with default weakly informative priors. Convergence was checked using the `shinystan` package (Muth, Oravecz, & Gabry, 2018). To take into account inter-individual variability and repeated measurement, we used mixed models including a random intercept and slope (represented by the number of blocks of 42 trials performed) for each individual. Thus, we limit our analysis to complete blocks of trials (all the model details are presented in the ESM). Additional analyses use nonparametric tests due to the non-independent nature of the data.

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

4. Study 1: stability of convention

In this first study, the baboons had to choose between pairs of coloured stimuli from seven possible colours. During the first period of the experiment, monkeys could see each other's responses through the transparent partition between them. We start by focusing on the proposer whose role is

to choose which of the two colours is to be selected. We found that the proposer's score was initially high (mean = 0.75, SEM = 0.02, min = 0.55, max = 0.95) and steadily increased at the beginning of the experiment ($\beta = 0.03$, 95%CI = [0.02,0.04]; Fig.3A). This increase in score was linked to the establishment of a hierarchy between colours (Fig.3B), some colours (such as yellow and orange) became progressively more chosen by the proposer than others (such as light and dark blue). We found that at the end of the experiment (the last two blocs of trials for each proposer) the difference in dominance rank between colours was highly correlated to the average score for that pair (Kendall, $N = 21$, $\tau = 0.71$, $z = 4.53$, $p < 0.001$), for instance the probability of success when orange and dark blue were presented together was on average 99% (a difference in Elo-score of 316) while it was 60% for light vs. dark blue (an Elo-score difference of 38).

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 average score remained high (Fig.4C). Most of the decisions taken by the responders are therefore based on the knowledge of the hierarchy and do not require visual access. However, we noticed that all the monkeys with very high score, above 85%, suffered from the introduction of the opaque partition, suggesting these individuals watched the proposer. To test this hypothesis, we divided the group into Low, Medium and High performing individuals based on their average score during the transparent condition and used a non-parametric correlation test to evaluate the relationship between the difference in Elo-score of the pair of colours and the difference in score between the transparent and opaque conditions (Fig.4D). We found that high performing monkeys used their knowledge of the hierarchy of colours when the Elo-score difference between the stimuli was high, and resorted to visual checking of their social partner when the difference was small (Kendall, $N = 5$, $\tau = -0.42$, $z = -2.66$, $p = 0.008$). In contrast, medium or low performing individuals seem to have only learned the dominance hierarchy of colours, and therefore have a lower score when the rank difference is small (Medium: Kendall, $N = 5$, $\tau = -0.13$, $z = -0.85$, $p = 0.40$; Low: Kendall, $N = 5$, $\tau = -0.06$, $z = -0.36$, $p = 0.72$).

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

5. Study 2: generalisation of the results

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

Figure 4: results from study 2. On the first row, results from experiment 2.1 and on the second row, results from experiment 2.2. A and C, evolution of score. B and D evolution of hierarchy. Legend is the same as in Fig.1 with the only difference that colours have been arbitrarily attributed to the black and white stimuli.

Monkeys could therefore establish a convention with different types of stimuli such as coloured squares, or black and white images. Next, in experiment 2.2, we questioned the importance of the transparent condition to establish the convention. Originally, we thought the monkeys would use the opportunity to see the action of their neighbour to choose the correct response, but the results showed that for a majority the introduction of the opaque partition had limited effect. We decided to question the necessity of having visual access to establish a convention by introducing five new black and white stimuli and performing the same experiment but with an opaque partition from the start. We found no qualitative differences between the experiment with a transparent or an opaque partition (Fig.4 and ESM). We noticed that the average score was lower and the evolution of the

dominance less noisy in the opaque condition, this is consistent with the fact that monkeys sometime rely on visual access, but it could also be due to differences in the stimuli we presented. Nonetheless, it appeared that individuals could rapidly establish a convention with or without visual access to their partner's responses.

6. Study 3: Arbitrariness of convention

A distinctive feature of conventions is their arbitrariness. In experiment 3.1, we tested the possibility of establishing an arbitrary convention by individually training monkeys to choose the five black and white stimuli of experiment 2.1 in the opposite order of dominance (we used an opaque partition so that monkeys had no visual access to their neighbours' behaviour). For instance, in experiment 2.1 we found that the "dog paw" was most frequently chosen when presented with the "leaf", we therefore trained the monkeys to make the opposite choice by rewarding the "leaf" and not the "paw". This is a strong test of arbitrariness because presumably the monkeys ordered the pairs according to their own preference, therefore, if an opposite convention is established and remain stable, this shows that even 'suboptimal' conventions can be maintained (a less stringent test would simply try to inverse two stimuli for instance).

All individuals were trained in the same reversed order. During training, we found, as expected, that the score was initially very low (for the first two blocks of trial, mean = 0.30, SE = 0.02, min = 0.19, max = 0.43). However, the performance rapidly improved as the monkeys learned to choose the correct stimuli for each pair (for the last two blocks of each individual, mean score = 0.72, SE = 0.05, min = 0.28, max = 0.99; see also Fig.S19). After the training phase we performed the same coordination experiment with the transparent partition as previously and found that the score remained high and showing no sign of decreasing ($\beta = 0.03$, 95%CI = [-0.03,0.08]). The hierarchy was also stable (Fig.S20) and in the opposite order of the one previously established (Fig.5). This shows that the established conventions are to some extent arbitrary.

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

366

367 Figure 5: Inversion of hierarchy between stimuli after training. First exposition refers to the
368 spontaneous Elo-scores obtained during experiment 2.1 and “after reversed training” to the Elo-
369 scores obtained after each individual had been trained on the reversed order.

370 Finally, in experiment 3.2, we wanted to test the impact that each baboon could have on the
371 establishment of convention based on their social relationships with others. We reasoned that well-
372 connected individuals could either be influential and change others or, on the contrary, be more
373 flexible and adapt to others. Following the same training procedure as previously, we trained three
374 individuals with the highest degree in their cluster on one hierarchy of five new stimuli and height
375 low-degree others in the reverse order (Fig.6). Once trained, we tested the establishment of a new
376 convention with a transparent partition as before.

Figure 6: Social network of the 11 individuals tested in the last experiment. Individuals with highest degree in their cluster (Mako, Violette, Ewine) were trained on the opposite convention compared to other individuals. The social network was obtained using the Force Atlas algorithm of Gephi (Bastian, Heymann, & Jacomy, 2009). Colours indicate different clusters, determined using Modularity classes. The thickness of the links represents the weight of the links between two individuals (equivalent to their number of trials performed together). The size of the nodes represents the weighted degree of the node (i.e. the sum of the link weights).

Individuals rapidly learned to choose the correct stimuli during training (for the last two blocks of each individual, mean score = 0.86, SE = 0.03, min = 0.66, max = 0.96; see also Fig.S24 for the evolution through time). During the coordination experiment, we found that the group converged on the convention of the low-degree individuals (Fig.7A) because high-degree individuals changed their behaviour more than did low-degree individuals. For instance, as can be seen on Fig.7B, the most dominant and least dominant stimuli were reversed for Violette (High degree) and did not change for Fana (Low degree; see Fig.S27 for the plots of each individual).

Figure 7: Evolution of Elo-scores trajectories for the entire group (A) and for the first 1000 trials of two individuals (B), Violette (high degree group) and Fana (low degree group).

7. Discussion and conclusion

In this series of experiments, we showed that when monkeys were faced with a coordination problem, they could spontaneously develop efficient arbitrary stable conventions. Conventions were efficient because the score improved with the emergence of conventions and because we found a direct relationship between the score and the hierarchy among the stimuli (Study 1 and 2.1). We showed that conventions were arbitrary and stable because after training to choose stimuli according to a new rule, monkeys could establish and maintain a new convention based on this new rule (Study 3.1). These three properties are defining features of human conventions and our results therefore complement a small number of field studies (discussed previously) showing that non-human primates can establish conventions akin to humans.

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

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

418 In our study monkeys established a new convention without any visual access to each other's
419 behaviour (experiment 2.2), therefore showing that imitation, or more generally observational
420 learning, is not necessary to establish conventions: in the opaque condition baboons were able to
421 establish a convention through positive reinforcement and knew nothing about the behaviour of their
422 conspecifics. However, we also found that the most successful monkeys were able to copy the
423 proposer when the task became difficult due to a small Elo-score difference between pairs of stimuli.
424 This is in agreement with the growing literature on social learning showing that individuals can learn
425 from the observation of conspecifics (Whiten, 2021) and with another study showing this effect with
426 touch-screen (Subiaul, Cantlon, Holloway, & Terrace, 2004).

427 According to Lewis (1969), there are three main sources explaining the emergence of
428 conventions: *agreement*, *saliency* and *precedence*. Agreement occurs when individuals can
429 communicate and form mutual expectations (i.e. agree on a course of action), for instance when
430 making an appointment. Conventions can also emerge when a solution is so salient that most
431 individuals tend towards that solution (i.e a preference system). Finally, conventions can emerge
432 through precedence: if a solution becomes more salient and remarkable because it was previously

successfully chosen (i.e. a regularity of behaviour). In the context of our study, agreement is unlikely to explain the emergence of conventions because monkeys (1) cannot explicitly agree on which colour to choose and moreover (2) continued to follow convention when the opaque partition prevented observation of their partner. On the other hand, monkeys can create conventions through a combination of saliency and precedence. Monkeys may all perceive certain stimuli as more salient than others (*saliency*) and the result of each trial also influence the stimuli future saliency (*precedence*).

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

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Ethics

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

Data Accessibility

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

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

Authors' Contributions

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

Competing Interests

We have no competing interests.

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