IDENTIFICATION OF THE SOCIAL AND COGNITIVE PROCESSES UNDERLYING HUMAN CUMULATIVE CULTURE

Dean, L.G.[1], Kendal, R.L.[2§], Schapiro, S.J.[3], Thierry, B.[4]
& Laland, K.N.[1§]

[1] Centre for Social Learning and Cognitive Evolution, School of Biology, University of St. Andrews, Queen's Terrace, St. Andrews, Fife, KY16 9TS, UK.

[2] Centre for the Coevolution of Biology and Culture, Department of Anthropology, University of Durham, U.K.

[3] Michale E. Keeling Center for Comparative Medicine and Research, The University of Texas MD Anderson Cancer Center, Bastrop, TX, USA.

[4] Département Ecologie, Physiologie et Ethologie, Institut Pluridisciplinaire Hubert Curien, Centre National de la Recherche Scientifique, Université de Strasbourg, Strasbourg, France.

[§] Correspondence: <rachel.kendal@durham.ac.uk>, <knl1@st-andrews.ac.uk>

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One sentence summary: **A comparative experimental investigation involving children, chimpanzees and capuchin monkeys isolates the critical social and cognitive capabilities underlying cumulative culture.**

The remarkable ecological and demographic success of humanity is largely attributed to our capacity for cumulative culture, with knowledge and technology accumulating over time, yet the social and cognitive capabilities supporting this remain unclear. In a comparative study of sequential problem solving, we provided groups of capuchin monkeys, chimpanzees and children with an experimental puzzlebox that could be solved in three stages to retrieve rewards of increasing desirability, to evaluate eight hypotheses concerning cumulative culture's origins. The success of the children, but not of the chimpanzees or capuchins, in reaching higher-level solutions was strongly associated with a package of socio-cognitive processes, including teaching through verbal instruction, imitation and prosociality, which were observed only in the children, and co-varied with performance.

The success of humanity, in colonizing virtually every terrestrial habitat on the planet and resolving countless ecological, social and technological challenges, is widely attributed to our species' unique capability for 'cumulative culture' – the extensive accumulation of knowledge, and iterative improvements in technology, over time (*1*,*2*). While many animals, especially mammals, birds and fishes, acquire knowledge and skills from others, often manifest in behavioral traditions, in no instance have these unambiguously exhibited 'ratcheting' in complexity (*2*). Given that the adaptive value of cumulative learning is well-established (*1,3,4*), the question as to why social learning should be widespread in nature, but cumulative culture so rare is a major evolutionary puzzle (*1,4-7*).

While claims have been made for cumulative culture in other species (*8-10*) the evidence is circumstantial, and contested (*2,5,6,11*). The resulting debate has spawned a large number of distinct hypotheses concerning the cognitive capabilities, or social conditions, thought to be necessary for cumulative culture. These explanations include a hypothesized critical dependency of cumulative culture on aspects of *social cognition* deemed to be exclusive to, or substantially enhanced in, humans, including teaching (henceforth hypothesis 1, or *H1*), language (*H2*), imitation (*H3*) and prosociality (*H4*) (*1,2,4,5,11-14*). Other explanations stress features of *social structure* that mitigate against the spread of superior solutions in animals other than humans, including scrounging (kleptoparasitism; *H5*), which can hinder social learning and de-motivate resource production (*15*), the tendency of dominant individuals to monopolise resources thereby preventing subordinates from learning (*H6; 16*), and a lack of attention to low-status inventors (*H7; 17-18*). A further (*non-social cognition*) hypothesis is that satisficing, or conservative behavior, hinders ratcheting in nonhumans (*H8*; *8,19*). Large social networks (*20,21*) may enhance cultural diversity and promote cumulative culture but we do not consider this hypothesis as it pre-supposes the existence of the necessary cognitive capabilities.

While cumulative culture has been investigated through historical analysis (*22*), in the psychological laboratory (*23*), and through experimentation in chimpanzees (*14*), hitherto there has been no extensive and rigorous comparative experimental investigation of the capacity for cumulative cultural learning, that simultaneously tests humans and other animals using the same apparatus, and that is capable of evaluating all of the aforementioned hypotheses. Here we present such an investigation.

We designed a puzzlebox (**Figure 1**) that could be solved at three stages of difficulty, with success at stage 2 building on stage 1, and similarly for stage 3. We presented appropriately scaled versions, under a variety of conditions, to groups of children (*N*=35. 8 groups of 3-4 year-olds from 3 nurseries in Fife, U.K.), chimpanzees (*Pan troglodytes; N*=74. 8 mixed juvenile and adult groups at the Michale E. Keeling Center for Comparative Medicine & Research, University of Texas, U.S.A) and capuchin monkeys (*Cebus apella;* 1 group over 2 years, Yr 1 *N*=22, Yr 2 *N*=18, at the Centre de Primatologie, Strasbourg, France). See SOM for methods. All stages could be completed through two parallel options, allowing us to investigate cooperation, tolerance and social learning at the task, whilst presentation in social groups allowed solutions to each level to spread to others. In Experiment 1 there were two conditions: an ‘open’ condition where groups could gain access to all stages, and a ‘scaffolded’ condition, where guards prevented access to the manipulandi associated with higher stages until performance at the lower stage reached criterion. In experiment 2, conducted only with chimpanzees, one female from each of four additional groups was isolated from her group and trained to use the puzzlebox to stage 3. The use of trained females of differing status as demonstrators allowed investigation of how social rank affected the spread of solutions.

Chimpanzees and capuchins were selected because the evidence for cultural traditions is as strong in these species as in any (*24,25*), maximising the chances of observing cumulative cultural learning. Moreover, chimpanzees, as our closest relative, provide an appropriate comparator to humans, with the performance of capuchins aiding interpretation of any chimpanzee-human differences. Children are widely used in comparative studies (*e.g. 26*) to help tease out the effects of culture, as adults have been greatly enculturated by society.

We anticipated that children, but not chimpanzees or capuchins, would exhibit evidence of cumulative cultural learning, and the study was designed to sort between alternative explanations for this. For a hypothesis to be deemed supported (strictly, not falsified) we specified that it should satisfy two criteria: (*i*) differences in the relevant predictor variable should covary with differences in species' mean performance in the cumulative task, in the predicted direction, and (*ii*) within-species variation in the relevant predictor should covary with variation in individual performance within species, in the predicted direction. Thus we used analyses of covariation, both between and within species, to reject causal hypotheses that were inconsistent with the data. We further assumed that the manner in which social or cognitive processes operate currently is qualitatively similar to the manner in which they operated in ancestral environments. Hence, while our study seeks to identify the proximate processes underlying cumulative cultural learning in contemporary populations, the same processes were potentially ancestral sources of selection.

Performance with the puzzlebox is summarized in **Figure 2A**. Following 30 hours of presentation of the task to each of four chimpanzee groups, only 1 of 33 individuals reached stage 3, with a further 4 having reached stage 2, and with each group having witnessed multiple solvers at stage 1 (Expt 1). Chimpanzee performance was not greatly enhanced by trained demonstrators (Expt 2), who performed stages 1-3 proficiently. A similar pattern is observed in the capuchins, where after 53 hours, no individual reached stage 3 and only two individuals reached stage 2. Thus the experiments provide no evidence for cumulative cultural learning in chimpanzees or capuchins. These findings stand in stark contrast to those of the children, where despite a far shorter exposure to the apparatus (2.5 hours), five of the eight groups had at least two individuals (out of maximum 5) who reached stage 3, with multiple solvers at stages 2 or 3 in all but two groups (see SOM).

Analyses revealed support for four of the eight hypotheses (**Figure 2B-E**), suggesting that teaching, communication, observational learning, and prosociality all played important roles in human cultural learning, but were absent or played an impoverished role in the learning of chimpanzees and capuchins.

A total of 23 unambiguous instances of teaching by direct instruction (i.e. referencing part of the puzzlebox) were observed ($\bar{x}$=0.69±0.32), exclusively in the children (**Fig. 2B**), all of which involved verbal instruction (e.g. "push that button there") and approximately one third involving gesture. A strong positive relationship was observed between the amount of instruction received and stage reached by a child (*Spearman's rho*=0.598, *P*=0.0001; *27*). Such an analysis fails to consider teaching precursors, or subtle processes similar to teaching, such as 'pedagogical cuing' (*28*) or 'scaffolding' (*29*). To explore whether chimpanzees or capuchins might facilitate learning in others (e.g. through enlisting offsprings' interest in the task), we examined rates of both provisioning and food-calling by 'knowledgeable' individuals. However, we observed substantially greater rates of tolerated theft of extracted food by mothers from offspring than vice-versa in chimpanzees (*Wilcoxon W*=16, *P*=0.026) and no tolerated theft in mother-infant pairs of capuchins. Moreover, neither chimpanzees (*Wilcoxon W*=6.5, *P*=0.77) nor capuchins (*W*=9, *P*=0.45) exhibited any difference in the rate of recruitment of others to the puzzlebox before, compared to immediately following, a food call, and low rates of calling were observed; in contrast, children that received verbal instruction outperformed those that did not (*Mann-Whitney U*=41, *P*=.002; **Fig. 2C**).

We also compared the rate at which individuals from each species, in their first response, or in the subsequent minute, performed a matching manipulation (e.g. copy push down button on left) to that observed being performed by another individual departing the box. Matching (Table S6, SOM) could constitute copying the actions of others (i.e. imitation) or making the same manipulandi move in the same way (i.e. emulation). Children alone performed more matching than non-matching manipulations (*Wilcoxon W*=163, *P*=0.003), they produced a significantly greater proportion of matching actions than both chimpanzees and capuchins (*Kruskal-Wallis* χ^2= 18.13, *df*=2, *P*=0.001; **Fig. 2D**), and the degree of matching they exhibited correlated positively with performance (*Spearman's rho*=0.41, *P*=0.01). We observed chimpanzee social learning at stage 1 (*Option-bias analysis*, χ^2= 941.6, *P*= 0.021, *30*) but not higher stages.

We hypothesized that if individuals voluntarily give rewards to others this signifies an understanding that others share the motivation of achieving the goal that they had achieved. We observed 215 altruistic events where a child spontaneously gave another child a retrieved reward ($\bar{x}$=6.14±2.32, 47% of children exhibited altruism), but not a single instance of the voluntary donation of food in either the chimpanzees or capuchins (**Fig. 2E**). The number of prosocial acts received covaried strongly with the stage that a child reached (*Spearman's rho*=0.54, *P*=0.001). Moreover, the proportion of manipulations that children performed at the same time as another individual was in proximity was significantly greater than in either chimpanzees or capuchins, indicating greater tolerance of others, cooperation and shared motivation in children.

The other four hypotheses failed to satisfy our criteria, providing little evidence that the capability for cumulative culture is affected by either social structure or non-social cognition. There was a positive, rather than the predicted negative, correlation between the amount of scrounging an individual falls victim to and performance in capuchins (*Spearman's rho*=0.71, *S*=511.6, *P*=0.0002), chimpanzees (*rho*=0.312, *S*=41052.3, *P*=0.008) and children (*rho*=0.8, *S*=1412.24, *P*=6.87x10- 9), and no sign that scrounging hindered performance (*H5*; **Fig. 2F**). Dominant children (*Wilcoxon W*=186, *P*=0.15) and chimpanzees (*ANOVA* $F_{2,72}$=3.49, *P*=0.036) did not monopolise the puzzlebox (*H6*), and while there was a positive correlation between rank and puzzlebox use among capuchins in 2007 (*Kruskal-Wallis* $\chi 2$=8.23, *df*=2, *P*=0.016), this was not repeated in 2008 ($\chi 2$=0.13, *df*=2, *P*=0.93) (**Fig. 2G**). When manipulating the box, low-rankers did not receive less attention (defined as having others within 1.5m of the task) than high-rankers (*H7*; **Fig. 2H**; capuchins 2007 *Kruskal-Wallis* $\chi 2$=2.49, *df*=2, *P*=0.29, 2008 $\chi 2$=2.08, *df*=2, *P*=0.35; chimpanzees *ANOVA* $F_{2,72}$=1.22, *P*=0.3; children *Wilcoxon W*=100, *P*=0.61), nor was there any evidence for satisficing or conservatism (*H8;* **Fig. 2I**; chimpanzees *Mann-Whitney U*=166.5, *P*=0.42; children *U*=163, *P*=0.54), with individuals continuing to manipulate the dials and buttons of the puzzlebox after they had found the solution to stage 1. In the open condition, where they received rewards at all stages, both chimpanzees and children manipulated the puzzlebox slightly more, rather than less, than individuals in the scaffolded condition, despite the latter being unrewarded at the previous stage(s). While we did not find a significant difference between the proportions of rewards scrounged at each stage in chimpanzees, they expressed clear and strong preferences for the three foodstuffs in pilot work, and olfactory holes in the doors allowed these foods to be detected in the apparatus prior to their extraction. Moreover, many of the chimpanzees performed failed attempts to access the foods by ‘termiting’ (inserting stalks through the olfactory holes), and all 29 cases involved an attempt to reach the highest stage food that was available. In the children and capuchins, more low-stage than high-stage rewards were scrounged, which reflects a greater motivation to retain high-grade rewards.

Thus, we found no support for the hypotheses that cumulative culture is absent in chimpanzees or capuchins because in these species the social transmission of superior solutions is hindered by scrounging, because dominant individuals monopolise key resources, because of a lack of attention to low-status innovators, because these animals satisfice, or because these animals were unable to discriminate higher-quality from lower-quality rewards. Nor can the results be easily dismissed as an artefact of captivity-testing, as wild chimpanzees and capuchins have been subjected to long-term studies that reveal no unambiguous evidence for cumulative culture (*24*,*25*). Likewise, our animals cannot be described as ‘dysfunctional’ as they have performed effectively in previous studies demonstrating social learning and tradition of non-cumulative tasks (*31*, *32*).

Closer inspection of the children's behaviour supports the conclusion that a package of social cognitive capabilities, encompassing teaching, largely through verbal instruction, as well as matching (e.g. imitation) and prosociality (altruism), was critical for performance at the highest level. **Table 1** reveals that all children that reached level 3 received at least one form of social support and 86% received at least two types. Conversely, children that did not benefit from social support generally performed poorly in the task. These data not only provide clear and strong evidence for a cumulative cultural capability in the children, but strongly link their elevated performance to their social cognition.

The puzzlebox experiment reveals clear and characteristic differences between the cumulative cultural learning, and patterns of social interaction, in children, chimpanzees and capuchin monkeys, highlighting socio-cognitive processes that may be important for cultural transmission to 'ratchet'. The children responded to the apparatus as a social exercise, manipulating the box together, matching the actions of others, facilitating learning in others through verbal instruction and gesture, and engaging in repeated prosocial acts of spontaneous gifts of the rewards they themselves retrieved. In contrast, the chimpanzees and capuchins appeared to interact with the apparatus solely as a means to procure resources for themselves, in an entirely self-serving manner, largely independent of the performance of others, and exhibiting restricted learning that appeared primarily asocial in character. Our findings, based on confirmation of predicted patterns of co-variation both between and within species, constitute strong support for the view (*2,11,12*) that cumulative culture requires a package of key psychological processes, specifically teaching through verbal instruction, imitation and prosocial tendencies, which are present in humans but are absent or impoverished in chimpanzees and capuchins. The claim that these socio-cognitive processes, rather than other effects, were directly responsible for the pattern of cumulative cultural learning observed in the children is supported by the positive relationships found between the amount of teaching, verbal instruction, and prosocial acts received, as well as the amount of observational learning engaged in, and stage reached (**Table 1**). We reject as improbable the alternative causal hypotheses, that performing well in the task caused elevated levels of the predictor variables, or that some unspecified factor elevated both performance and the predictors. It is not clear why success in solving the task should cause children to imitate, be taught by, or receive rewards from, others, nor how an unspecified third variable might account for our within-species data. For instance, while we cannot rule out the possibility that the relationship between imitation and performance reflects the child’s cognitive ability, this explanation cannot account for the relationships of both teaching and prosociality with performance, since in both cases the donor (of knowledge or reward) is a different individual to the learner. The most likely explanation is that aspects of human social cognition are directly responsible for the cumulative culture capability.

Human cultural traditions accumulate refinements over time, thereby producing both technology and other cultural achievements of astonishing complexity and diversity unprecedented in the rest of nature. Although numerous hypotheses have been proposed for this phenomenon, the explanation has for many years remained elusive. Our experiment provides a particularly clear answer to this conundrum, providing strong support for the position advanced by Tomasello and colleagues (*2,11,12,33*), that “human social learners focus to a much greater degree than other non-human primates on the actual actions performed by others …[and]… that uniquely human forms of cooperation ... teaching and norms of conformity contribute to the cultural ratchet (*11, p2413*)". These findings pave the way for an exciting avenue of research regarding when and why this particular 'package' of other regarding socio-cognitive capacities evolved.

Table 1. The number (and percentage) of children reaching each stage, together with the amount of teaching, matching (e.g. imitation) and prosociality (altruism) exhibited.

Stage reached	Number of individuals (from *N* groups)	Number that received teaching	Number with more matching than non-matching manipulations	Number that received altruism	Number that received no social support
0	8 (5)	0	1 (12.5%)	0	7 (87.5%)
1	8 (3)	0	4 (50%)	4 (50%)	3 (37.5%)
2	4 (3)	1 (25%)	1 (25%)	2 (50%)	1 (25%)
3	15 (5)	9 (60%)	11 (73%)	11 (73%)	0

Figure captions

Figure 1. A. The cumulative culture puzzlebox, which could be solved at three sequential stages, each building on the preceding stage. B. Illustration of puzzlebox use. Stage 1 required individuals to push a door in the horizontal plane, to reveal a chute through which a low-grade reward was delivered. Stage 2 required individuals to depress a button and slide the door further, to reveal a second chute for a medium-grade reward. Stage 3 required the solver to rotate a dial, releasing the door to slide further still, and reveal a third chute containing a high-grade reward. All stages could be completed through two parallel options (alternative doors could be slid left or right at stage 1, alternative buttons at the top or bottom could be depressed at stage 2, and alternative coloured finger-holes enabled the dial at stage 3), with sets of 3 chutes on both left and right sides. This two-action, two-option design aided evaluation of alternative social learning mechanisms, and allowed two individuals to operate the puzzlebox simultaneously. Replenishment of the chutes by the experimenter allowed the apparatus to be continuously used for long periods. Pilot work established an unambiguous ascendancy in the desirability of reward with stage (food stage 1=carrot, 2=apple, 3=grapes for chimpanzees/capuchins, stickers of increasing size and attractiveness for children).

Figure 2. A. Higher-level (stages 2 and 3) was exceptionally rare or absent in capuchins and chimpanzees but common in children. B. 23 unambiguous instances of teaching, by direct instruction, were observed, exclusively in human children. C. In neither chimpanzees nor capuchins was there greater recruitment to the task after, compared to before, a food call. Conversely, children that received verbal instruction

outperformed those that did not. D. Children alone performed more matching than non-matching manipulations, and produced a greater proportion of matching actions than chimpanzees and capuchins. E. 215 altruistic events were observed (giving an extracted reward to others), exclusively in children. F. There was no evidence that scrounging hindered performance in any species, whilst children that were victims of scrounging outperformed children that were not. G. Dominant children and chimpanzees did not monopolise the task, and high-ranking capuchins monopolised the puzzlebox in 2007 but not 2008. H. Low-rankers did not receive less attention than high-rankers, when manipulating the task. I. In the open condition, where they received rewards at all stages, neither chimpanzees nor children manipulated the puzzlebox less than individuals in the scaffolded condition. In G-H capuchin and chimpanzee data analysed in three (high, mid, low) rank categories.

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27. We conducted two classes of analyses, cross-species comparisons and single-species analyses exploring the relationship between a predictor variable and performance. For the latter analyses, to render the distribution continuous we computed an ‘achievement rank’ by combining stage-reached and number of successful manipulations data (see SOM for details).

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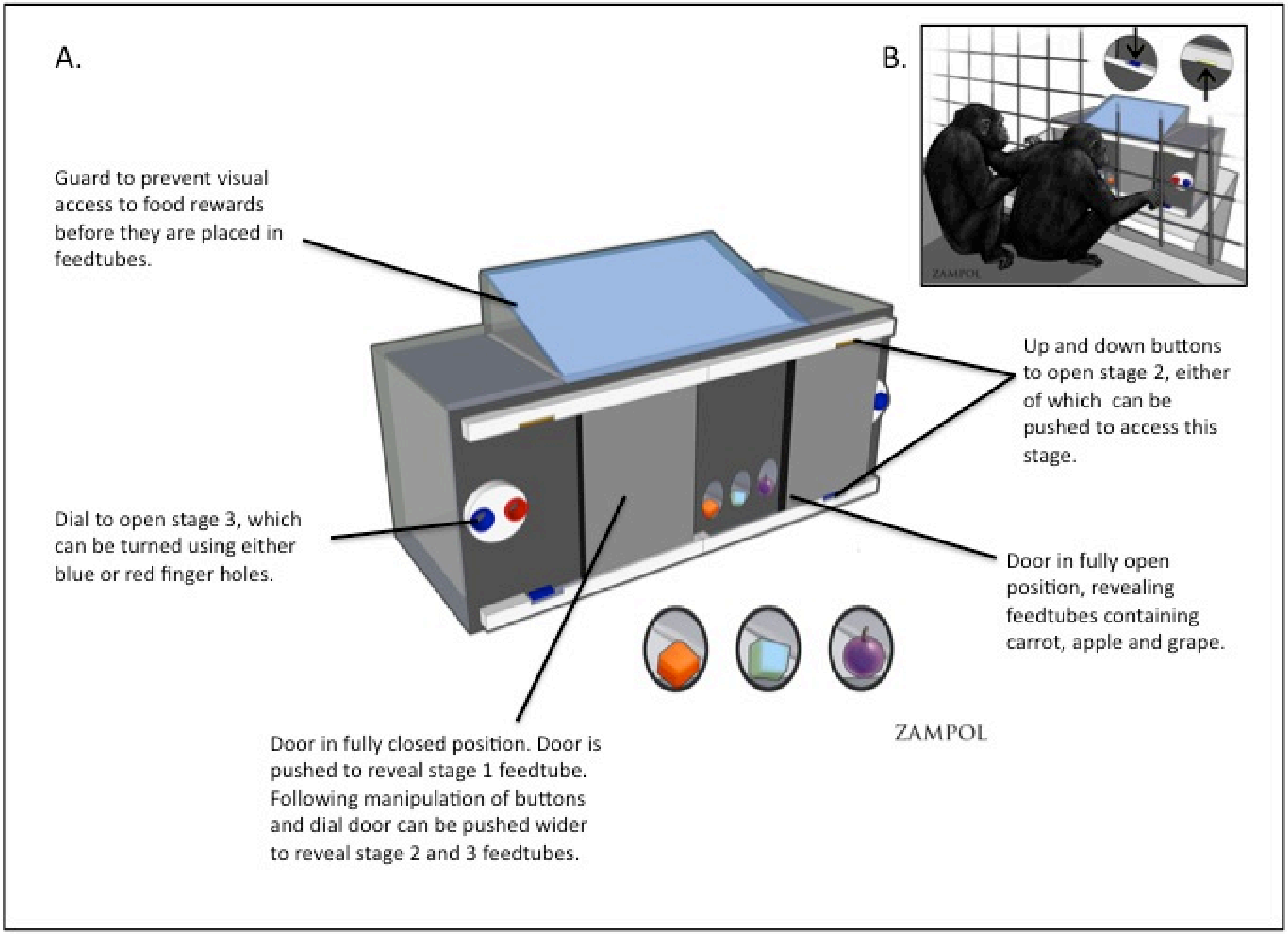


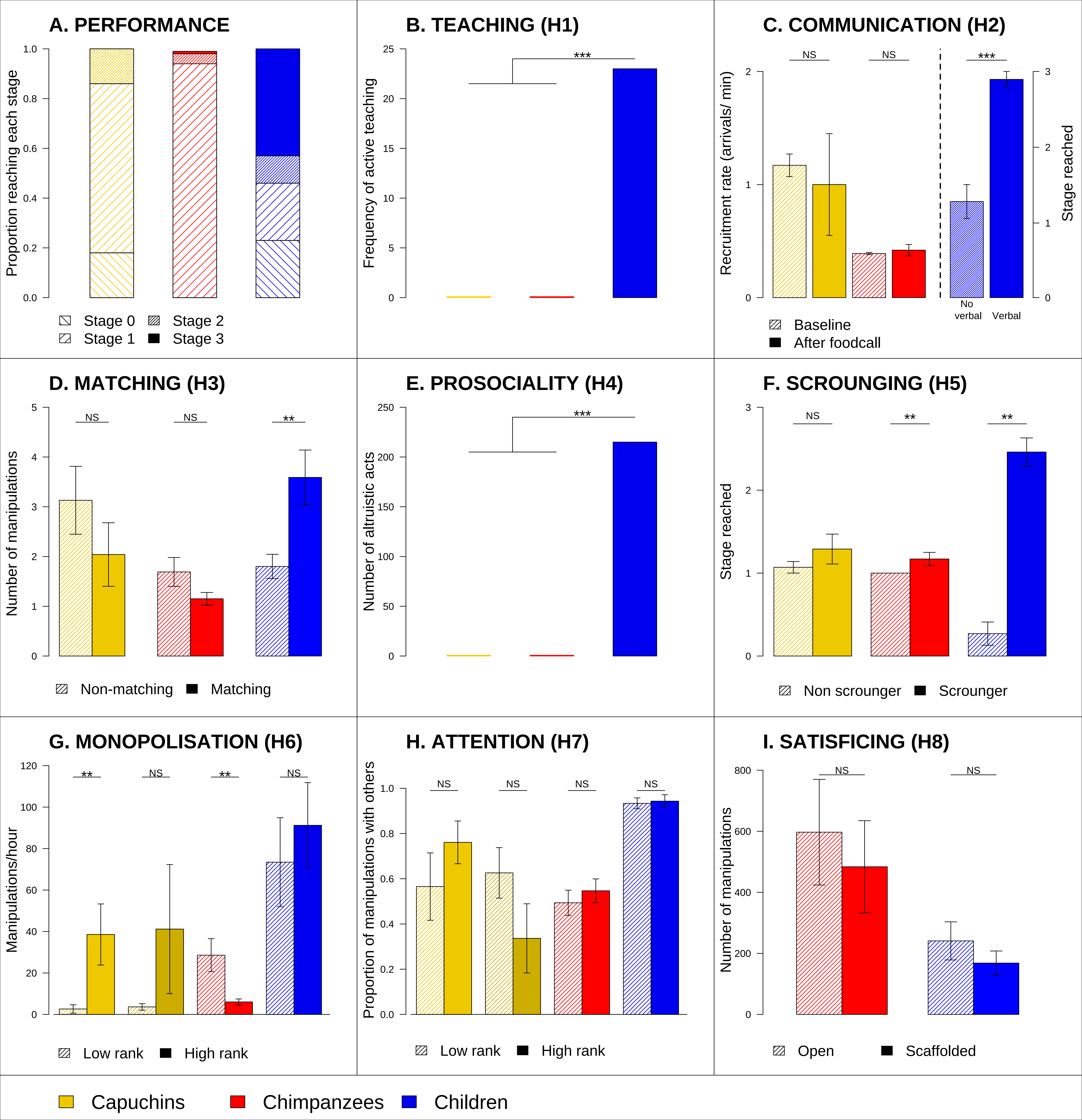
Guard to prevent visual access to food rewards before they are placed in feedtubes.

Dial to open stage 3, which can be turned using either blue or red finger holes.

Up and down buttons to open stage 2, either of which can be pushed to access this stage.

Door in fully open position, revealing feedtubes containing carrot, apple and grape.

Door in fully closed position. Door is pushed to reveal stage 1 feedtube. Following manipulation of buttons and dial door can be pushed wider to reveal stage 2 and 3 feedtubes.


A. PERFORMANCE
Proportion reaching each stage
1.0
0.8
0.6
0.4
0.2
0.0
▧ Stage 0
▨ Stage 1
▩ Stage 2
■ Stage 3
B. TEACHING (H1)
Frequency of active teaching
25
20
15
10
5
0
***
C. COMMUNICATION (H2)
Recruitment rate (arrivals/ min)
Stage reached
NS
NS
***
2
1
0
3
2
1
0
No verbal
Verbal
▨ Baseline
■ After foodcall
D. MATCHING (H3)
Number of manipulations
5
4
3
2
1
0
NS
NS
**
▨ Non-matching
■ Matching
E. PROSOCIALITY (H4)
Number of altruistic acts
250
200
150
100
50
0
***
F. SCROUNGING (H5)
Stage reached
3
2
1
0
NS
**
**
▨ Non scrounger
■ Scrounger
G. MONOPOLISATION (H6)
Manipulations/hour
120
100
80
60
40
20
0
**
NS
**
NS
▨ Low rank
■ High rank
H. ATTENTION (H7)
Proportion of manipulations with others
1.0
0.8
0.6
0.4
0.2
0.0
NS
NS
NS
NS
▨ Low rank
■ High rank
I. SATISFICING (H8)
Number of manipulations
800
600
400
200
0
NS
NS
▨ Open
■ Scaffolded
🟨 Capuchins
🟥 Chimpanzees
🟦 Children