Report

Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates

Federica Amici,[1,2,3,4] Filippo Aureli,[1,*] and Josep Call[2,*]

[1]Research Centre in Evolutionary Anthropology and Palaeoecology
School of Biological and Earth Sciences
Liverpool John Moores University
James Parsons Building
Byrom Street
Liverpool L3 3AF
United Kingdom
[2]Department of Comparative and Developmental Psychology
Max Planck Institute for Evolutionary Anthropology
Deutscher Platz 6
04103 Leipzig
Germany
[3]Unit of Cognitive Primatology and Primate Center
Institute of Cognitive Sciences and Technologies
CNR
Via Ulisse Aldrovandi 16/b
00197 Rome
Italy
[4]Research Group Behavioural Biology
Ethologie Station
Padualaan 8
De Uithof, 3584CH Utrecht
the Netherlands

Summary

The Machiavellian Intelligence or Social Brain Hypothesis explains the evolution of increased brain size as mainly driven by living in complex organized social systems [1–4] in which individuals represent "moving targets" who can adopt multiple strategies to respond to one another [5]. Frequently splitting and merging in subgroups of variable composition (fission-fusion or FF dynamics) has been proposed as one aspect of social complexity ([2, 6–9]; compare with [10]) that may be associated with an enhancement of cognitive skills like inhibition [11], which allows the suppression of prepotent but ineffective responses in a changing social environment [7]. We compared the performance of primates experiencing high levels of FF dynamics (chimpanzees, bonobos, orangutans, and spider monkeys) to that of species living in more cohesive groups (gorillas, capuchin monkeys, and long-tailed macaques) [12–13] on five inhibition tasks. Testing species differing in diet, phylogenetic relatedness, and levels of FF dynamics allowed us to contrast ecological, phylogenetic, and socioecological explanations for interspecific differences. Spider monkeys performed at levels comparable to chimpanzees, bonobos, and orangutans, and better than gorillas. A two-cluster analysis grouped all species with higher levels of FF dynamics together. These findings confirmed that enhanced inhibitory skills are positively associated with FF dynamics, more than to phylogenetic relations or feeding ecology.

*Correspondence: f.aureli@ljmu.ac.uk (F.A.), call@eva.mpg.de (J.C.)

Results and Discussion

We administered a battery of five tasks that assessed motor and temporal aspects of inhibition (A-not-B, middle-cup, Plexiglas-hole, swing-door, and delay-of-gratification tasks). The basic procedure consisted of our presenting two or more alternatives for the subjects to choose from (Figure 1). Table 1 presents the mean corrected percentages of correct choices (or the indifference point reached in the delay-of-gratification task) and the relative rank of each species in each task, as well as the mean overall rank across all tasks for each species. The individual scores obtained significantly differed across species in four of the five tasks (Kruskall-Wallis tests: p < 0.02; see Table 1).

There were significant differences between species on the mean individual ranks in performance across the five tasks (Kruskall-Wallis test: $\chi^2 = 31.05$, df = 6, p < 0.001, n = 76). Chimpanzees and spider monkeys significantly outperformed gorillas, capuchin monkeys, and long-tailed macaques; bonobos significantly outperformed capuchin monkeys and long-tailed macaques; and orangutans significantly outperformed long-tailed macaques (see Figure S1, available online, for an illustration of all pairwise comparisons).

Figure 2 presents the dendrogram that resulted from a cluster analysis based on the mean of the ranks in each task for each species. Spider monkeys clustered with great apes characterized by high levels of fission-fusion (FF) dynamics, whereas gorillas clustered with the two remaining monkey species. It is noteworthy that the species that associated most closely were the long-tailed macaques and capuchin monkeys on one side and the spider monkeys and bonobos on the other side. When opting for a two-cluster solution, we found that all the species with higher levels of FF dynamics were grouped together, regardless of phylogenetic relatedness.

We identified three possible phylogenetically independent pairwise comparisons [14, 15] involving *Pan* versus *Gorilla*, *Pongo* versus *Macaca*, and *Ateles* versus *Cebus*. Across the five tasks and within each pair, we found that taxa with higher levels of FF performed better than taxa living in more cohesive groups in 11 cases, whereas the opposite was true only twice (and in two cases no difference was found).

Table 2 presents the comparisons across monkey species on the basis of the whole data set (also see the Supplemental Data for the number of trials in each task). The results of this analysis confirmed the previous findings. Species significantly differed in the performance on each of the five tasks (Kruskall-Wallis tests: p < 0.05; see Table 2). Pairwise comparisons revealed that spider monkeys significantly outperformed capuchin monkeys and long-tailed macaques in two and four tasks, respectively, whereas capuchin monkeys significantly outperformed long-tailed macaques in three tasks (see Table 2).

Our results supported the hypothesis that high levels of FF dynamics are associated with higher behavioral flexibility, measured by means of inhibitory control. This finding does not imply that high levels of FF caused the enhancement of inhibitory skills, given that it is also possible that the enhancement, caused by other factors, might have allowed the

1. A not B

2. Middle cup

3. Plexiglas hole

4. Swing door

5. Delay of gratification
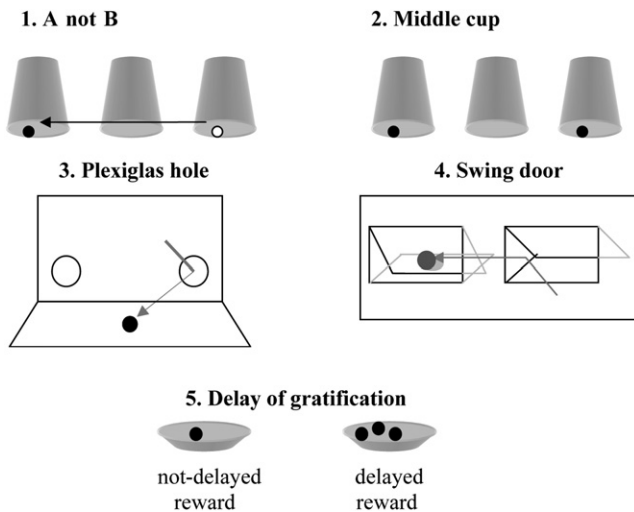
not-delayed reward

delayed reward

Figure 1. Illustration of the Experimental Set-Up for the Five Tasks

development of more flexible social systems [7]. It is also important to highlight that all species showed inhibitory skills, the only difference consisting of the level of inhibition across different species, with an overall enhancement in species with higher levels of FF dynamics. It is unlikely that the interspecific differences in performance were due to interspecific differences in perceptual or motor skills rather than differences in inhibitory control because all tasks were selected on the basis of their low perceptual and motor demands. Additionally, some tasks included control conditions whose manipulative, perceptual, and representational requirements were identical to the experimental condition except for the inhibition component. Similarly, we think that it is very unlikely that our results are due to group differences regarding the individuals' housing or experimental histories because all apes were housed under virtually identical housing conditions in the same center and received the same experimental protocols, yet we found consistent differences between gorillas and the other apes.

Moreover, spider monkeys, which were the only experimentally naive individuals, outperformed capuchins and long-tailed macaques. Although one could argue that previous experience might have interfered with the capuchins' and long-tailed macaques' performance, this explanation cannot account for the good performance of the chimpanzees, bonobos, and orangutans, which, like the capuchins and macaques, also had some experimental experience. Unless one speculates that experience differentially affects chimpanzees, bonobos, and orangutans compared to gorillas, capuchins, and macaques, this argument simply cannot explain our data.

The lower general performance of capuchin monkeys, long-tailed macaques, and gorillas in the five tasks compared to that of spider monkeys and the other three great apes makes an explanation based on phylogenetic relatedness (monkeys versus apes) untenable. This view is also supported by our three phylogenetically independent pairwise comparisons [14, 15]. Similarly, dietary considerations cannot explain these results either. Recent studies have indeed explained interspecific differences in inhibitory skills in terms of different ecologies and foraging patterns, proposing feeding ecology as a selective pressure for the enhancement of inhibitory skills [16–18]. However, differences in feeding ecology and dietary preferences alone cannot explain our results because frugivorous capuchin monkeys scored lower than folivorous gorillas. Overall, socioecological considerations and, more specifically, levels of FF dynamics seem to be the best predictors of the species' performance.

Comparative research on corvids showed that group-living species like pinyon jays outperform more solitary species in reversal learning (a task typically used to measure inhibitory control) [19]. The relationship between degree of sociality and performance on the task is likely to be linked to interspecific differences in behavioral flexibility, although it is unclear whether pinyon jays experience high levels of FF dynamics. Interestingly, pinyon jays outperform more solitary species like scrub jays in problems of transitive inference of dominance rank [20], which is one of the abilities that has been hypothesized to be enhanced in species with higher levels of FF dynamics [7]. These similarities may further support the idea of

Table 1. Mean Score, Number of Trials, Performance Rank, and Statistical Comparisons across Species for Each Task

Species	A not B (1 trial)		Middle Cup (2 trials)		Plexiglas Hole (2 trials)		Swing Door (10 trials)		Delay of Gratification[a]		Mean rank
	Score	Rank	Score	Rank	Score	Rank	Score	Rank	Score	Rank	
Chimpanzee	100.0 ± 0	2	56.3 ± 14.8	4	93.8 ± 6.3	2	10.0 ± 6.6	2	124 ± 11	1	2.2
Orangutan	83.3 ± 16.7	5	83.3 ± 30.7	1	100.0 ± 0	1	38.6 ± 12.2	1	50 ± 9	4	2.4
Bonobo	100.0 ± 0	2	75.0 ± 14.4	3	87.5 ± 12.5	3	0	5.5	74 ± 9	3	3.3
Spider monkey	93.3 ± 6.7	4	79.4 ± 6.2	2	66.7 ± 16.7	5	0	5.5	76 ± 8	2	3.7
Gorilla	100.0 ± 0	2	21.4 ± 14.9	7	41.7 ± 15.4	6	8.3 ± 8.3	3	44 ± 11	5	4.6
Capuchin monkey	79.0 ± 9.6	6	34.2 ± 9.4	6	78.1 ± 7.9	4	0	5.5	22 ± 3	7	5.7
Long-tailed macaque	75.0 ± 17.9	7	45.8 ± 14.4	5	4.2 ± 4.2	7	0	5.5	24 ± 4	6	6.1
Kruskall-Wallis test: χ^2	5.239		15.576		36.771		34.558		44.162		
p values (df = 6)	0.524		0.016		<0.001		<0.001		<0.001		
Pairwise comparisons	(−)		S > G = CM = M		C = O = S = B = CM > M; O > G		O > S = CM = M		B = O = S > CM = M; C > all		

Mean score (±SE) for each task and species. Species are also ranked according to the mean score obtained in each task, and the mean rank of all the tasks is shown for each species. Also shown are the comparison across species and the pairwise comparisons for the individual scores obtained in each of the task. The scores represent the corrected percent of correct choices for the A-not-B and middle-cup tasks, the percent of correct choices for the Plexiglas-hole and swing-door tasks, and the reached indifference point for the delay-of-gratification task. C = Chimpanzee, O = Orangutan, B = Bonobo, S = Spider monkey, G = Gorilla, CM = Capuchin monkey, M = Long-tailed macaque.
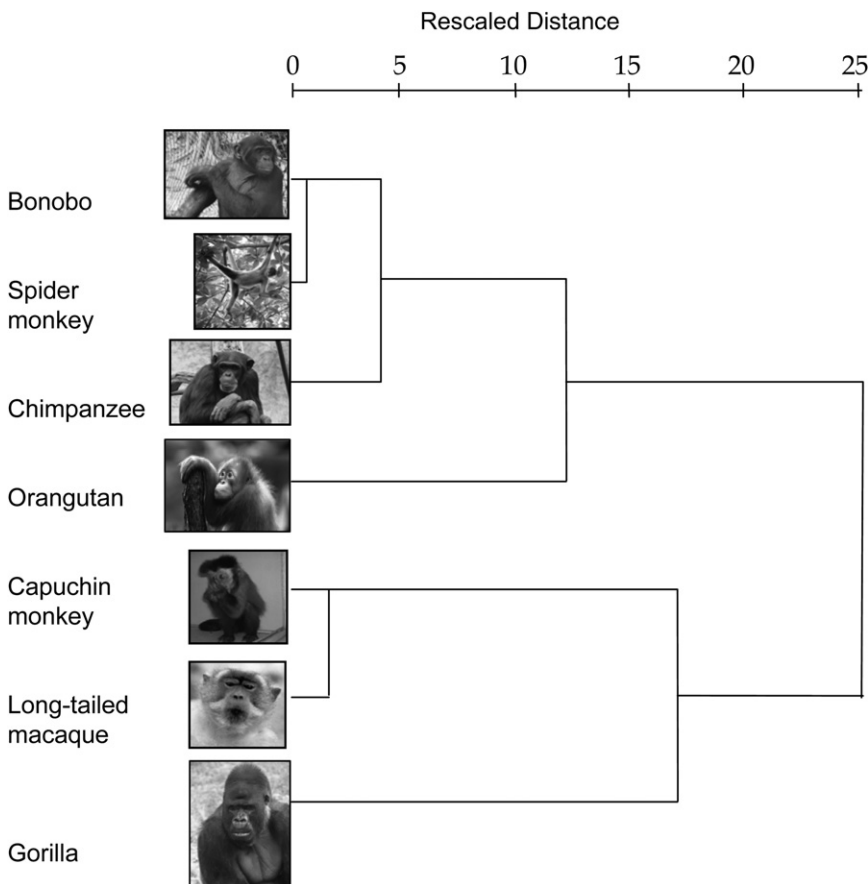[a] Owing to the delay-of-gratification procedure, this task did not entail a fixed number of trials.

Figure 2. Dendogram Resulting from a Hierarchical Cluster Analysis that Uses Average Linkage between Groups

are among the most likely to display some patterns of FF dynamics [25]. Capuchin monkeys were the second-lowest performers (Table 1). This is remarkable because capuchin monkeys excel in several other types of tasks [26, 27]. The variation in our results among monkey (and ape) species suggests that caution is required when using only a few species to draw conclusions about monkey-ape cognitive differences.

There are at least three directions in which one could further test the hypothesis that higher levels of FF dynamics are linked to enhanced behavioral flexibility and specific cognitive skills. First, Aureli et al. [7] hypothesized that other cognitive skills (including memory for temporal and spatial information, as well as inferential and analogical skills) may also differ between species with different levels of FF dynamics. In this vein, it would be interesting to investigate how spider monkeys perform in multiple tasks requiring these cognitive abilities when compared to other monkeys and great apes. Second, future research could extend the hypothesis beyond primates by testing nonprimate species experiencing high levels of FF dynamics (such as elephants, spotted hyenas, sperm whales, bottle-nosed dolphins, and appropriate bird species) and comparing them to closely related species living in more cohesive groups [7]. Third, the epigenesis of behavioral flexibility and inhibition is another important aspect that remains unexplored. For example, would macaques or capuchin monkeys raised in a society with higher levels of FF dynamics develop better inhibitory skills? Although this question may seem farfetched, similar processes have already been documented, with young macaques increasing their reconciliation levels if raised with individuals of a different, more conciliatory macaque species [28].

an evolutionary convergence in the cognition of corvids and some primate species [21].

This is not the first time that the spider monkeys' performance in cognitive tasks has been shown to be similar to that of orangutan, chimpanzees, and bonobos. The meta-analysis by Deaner et al. [22] showed that spider monkeys performed well in a variety of tasks and considerably better than gorillas and other monkey species. Most of the tasks included in their meta-analysis involved learning and problem solving, not inhibition per se. In the present study, we could specifically relate the spider monkeys' performance to inhibitory skills, although we cannot exclude the possibility that other cognitive skills might also be especially enhanced in species with higher levels of FF dynamics (see below). Despite the remarkable results obtained, Deaner et al. [22] did not relate spider monkeys' enhanced performance to socioecological factors. The overall performance of spider monkeys in our tasks, along with their characteristics (being monkeys and living in groups with high levels of FF dynamics), highlights the fact that they are a key species for testing hypotheses related to the role of FF dynamics in the enhancement of cognitive skills.

Long-tailed macaques were the species with the poorest performance. This result is notable, considering that many of the studies comparing monkeys and apes are based on the performance of long-tailed (or rhesus) macaques and chimpanzees, the two species that occupied the opposite extremes in the distribution of our results (Table 1). It is possible that other macaque species would perform better than long-tailed macaques, given that important differences among macaque species have been described [23, 24]. However, this seems unlikely because within macaque species, long-tailed macaques

Experimental Procedures

We administered a battery of five tasks that assessed motor and temporal aspects of inhibition to 18 spider monkeys (*Ateles geoffroyi*), 27 brown capuchin monkeys (*Cebus apella*), 12 long-tailed macaques (*Macaca fascicularis*), 7 gorillas (*Gorilla gorilla*), 10 orangutans (*Pongo pygmaeus*), 8 chimpanzees (*Pan troglodytes*), and 4 bonobos (*Pan paniscus*) (see the Supplemental Data for additional details on the subjects). The experiments reported here complied with German laws on animal experimentation and were originally approved by the joint committee of the Max Planck Institute for Evolutionary Anthropology and the Zoo Leipzig. The remaining institutions where this research was conducted also approved the experimental protocols. The basic procedure consisted of our presenting two or more alternatives for the subjects to choose from (Figure 1). In some cases, this entailed subjects' retrieving hidden rewards from under three cups (A not B, middle cup), reaching for a single visible reward from one of two different locations (plexiglas hole, swing door), or selecting between two visible rewards (delay of gratification). Subjects received the reward if they selected a baited cup, successfully avoided the barrier that blocked the direct access

Table 2. Mean Score for All Trials, Number of Trials, and Statistical Comparisons across Monkey Species for Each Task

Species	Task				
	A not B (18 trials)	Middle Cup (18 trials)	Plexiglas Hole (18 trials)	Swing Door (20 trials)	Delay of Gratification[a]
Spider monkey	91.8 ± 3.3	78.9 ± 4.5	85.3 ± 4.9	4.6 ± 1.8	76 ± 8
Capuchin monkey	85.4 ± 3.1	60.3 ± 5.2	90.4 ± 2.7	1.7 ± 1.7	22 ± 3
Long-tailed macaque	80.1 ± 4.5	37.8 ± 7.4	28.2 ± 8.7	0	24 ± 4
Kruskall-Wallis test: χ^2	6.371	15.448	23.372	7.465	22.910
p values (df = 2)	0.041	<0.001	<0.001	0.031	<0.001
Pairwise comparisons	S > M	S > C > M	C = S > M	(−)	S > C = M

Mean score (± SE) for each task across monkey species in all trials, statistical comparison across species, and pairwise comparisons for the individual scores obtained in each of the task (see Table 1 for further details). S = Spider monkey, C = Capuchin monkey, M = Long-tailed macaque.
[a] Owing to the delay-of-gratification procedure, this task did not entail a fixed number of trials.

to the reward, or selected the delayed visible reward. Some of the ape data had been previously collected as part of other studies ([18, 29, 30]; J. Call, unpublished data). In those cases, we used those data for interspecific comparisons because they represented the first time that subjects had been confronted with the tasks used here. Tables 1 and 2 report the number of trials for each task.

A-not-B Task
In a procedure based on that of Piaget [31], subjects saw three aligned cups and a reward that was placed under one of the two cups that occupied an exterior position (cup A), and they were allowed to retrieve the reward for three consecutive trials. On the fourth trial, subjects saw the reward placed under cup A once more, but the experimenter immediately took it out and moved it to the other exterior cup (cup B), in full view of the subject. Subjects were then allowed to search for the reward. This task tests whether subjects can refrain from choosing the cup under which they previously found food but that has been recently emptied.

Middle-Cup Task
In a procedure based on that of Call [32], subjects saw three aligned cups and two rewards that were placed under two of the cups, and they were allowed to retrieve the rewards. In control trials, the experimenter baited one of the exterior cups and the middle cup. In experimental trials, the experimenter baited both exterior cups, leaving the middle cup empty. This task tests whether subjects can refrain from choosing an empty cup that is close to a cup from which they have just retrieved a reward.

Plexiglas-Hole Task
For six consecutive trials, subjects saw a reward alternatively placed in front of one of the two holes made on a transparent Plexiglas panel standing upright on the ground between the subject and the reward. On the seventh trial, the reward was instead placed between the two holes. This task tests whether subjects can refrain from reaching toward the reward through the Plexiglas and instead take a detour movement through one of the two holes.

Swing-Door Task
In a procedure based on that of Vlamings [30], subjects were presented with a transparent Plexiglas panel with two holes cut on it that was covered by two swinging transparent doors fixed on their upper sides. The holes could only be accessed by pushing the doors forward. A reward was placed behind one of the doors on a ledge, but attempts to reach for it by pushing the door made the reward fall backward and out of reach. This task tests whether subjects can refrain from reaching the reward directly and instead open the nonbaited door to grab the reward from behind.

Delay-of-Gratification Task
In a procedure based on that of Rosati et al. [33], subjects were presented with two different amounts of food, a smaller immediately available one and a larger one that was available after a varying delay of time. The delay varied according to the subject's performance in the previous sessions and was held constant throughout a session. Subjects were tested until they equally valued the smaller immediate reward and the larger delayed reward, i.e., when the mean delay for the larger reward of the last five completed sessions did not differ from the mean delay of the preceding five sessions by more than 10% and all the delays in the last five sessions were within a 30 s range. The mean delay of the last five sessions was considered the estimation of the subject's indifference point. This task evaluates the subjects' discounting behavior by testing whether they can refrain from

reaching for a smaller immediate reward to obtain a larger delayed one. (See the Supplemental Data for additional details on each of the tasks).

Data Scoring
All trials were videotaped, scored live, and later checked against the videotapes. For the delay-of-gratification task, we scored the subjects' choice in each trial until the indifference point was reached. For all the other tasks, we scored whether subjects made the successful choice in each trial. A second observer coded 20% of the trials for each task to assess interobserver reliability, which was excellent (Cohen's κ ranging from .78 to .93 in the different tasks).

Statistical Analyses
Our main analyses were based on the initial trials administered in each task (except for the delay-of-gratification task) because this allowed us to compare across all species and minimized the effect of learning on performance. For those tasks in which subjects had to remember the location of a hidden reward (A-not-B and middle-cup tasks), we corrected the percentage of correct experimental choices by dividing it by the percentage of correct choices in a control condition, in order to eliminate the potential effect of differential memory span across species. We used the individual (corrected) percentage of correct choices or the indifference point reached (for the delay-of-gratification task) to analyze interspecific differences in each task with the Kruskal-Wallis test. When the result of the Kruskal-Wallis test was significant, we used Mann-Whitney tests for pairwise comparisons [34]. We then ranked all the subjects according to their performance in each task and used the mean rank over the five tasks to test overall differences among the species (Figure S1). We also ranked all the subjects according to the mean species performance in the five tasks (Table 1). We calculated the sum of the squared Euclidean distance across the ranks of the five tasks for each pair of species. For instance, the distance between bonobos and spider monkeys was $(2−4)^2 + (3−2)^2 + (3−5)^2 + (5.5−5.5)^2 + (3−2)^2 = 10$. We used the resulting matrix to perform a cluster analysis, using the average linkage between groups as the agglomeration method (Figure 2). Finally, we compared the three monkey species by using their scores in the whole data set (including more trials than those used for the comparisons with the great apes; see Supplemental Experimental Procedures) to assess whether interspecific differences observed in the initial trials were also apparent after additional testing (Table 2). All tests used exact and two-tailed probability. The α level was set at 0.05, but in the case of multiple pairwise comparisons, it was decreased to 0.01.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, one figure, and one table and can be found with this article online at http://www.current-biology.com/cgi/content/full/18/18/1415/DC1/.

References

1. Byrne, R.W., and Whiten, A. (1988). Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans (Oxford: Oxford University Press).
2. Dunbar, R.I.M. (2003). Why are apes so smart? In Primate Life Histories and Socioecology, P.M. Kappeler and M.E. Pereira, eds. (Chicago: University of Chicago Press), pp. 285–298.
3. Dunbar, R.I.M., and Shultz, S. (2007). Evolution in the social brain. Science 317, 1344–1347.
4. Dunbar, R.I.M. (1998). The social brain hypothesis. Evol. Anthropol. 6, 178–190.
5. Byrne, R.W., and Bates, L.A. (2007). Sociality, evolution and cognition. Curr. Biol. 17, R714–R723.
6. Barrett, L., Henzi, P., and Dunbar, R. (2003). Primate cognition: From 'what now?' to 'what if?'. Trends Cogn. Sci. 7, 494–497.
7. Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, R.I.M., Henzi, S.P., et al. Fission-fusion dynamics: New research frameworks. Curr. Anthropol., in press.
8. Milton, K. (2000). Quo vadis? Tactics of food search and group movement in primates and other animals. In On the Move: How and Why Animals Travel in Groups, S. Boinski and P.A. Garber, eds. (Chicago: University of Chicago Press), pp. 375–417.
9. Boesch, C., and Boesch-Achermann, H. (2000). The Chimpanzees of the Taï Forest (Oxford: Oxford University Press).
10. Kummer, H. (1971). Primate Societies – Group Techniques of Ecological Adaptation (Chicago: Aldine Publishing Company).
11. Santos, L.R., Ericson, B.N., and Hauser, M.D. (1999). Constraints on problem solving and inhibition: Object retrieval in cotton-top tamarins (Saguinus oedipus oedipus). J. Comp. Psychol. 113, 186–193.
12. Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., and Struhsaker, T.T. (1987). Primate Societies (Chicago: University of Chicago Press).
13. Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M., and Bearder, S.K. (2006). Primates in Perspective (Oxford: Oxford University Press).
14. Maddison, W.P. (2000). Testing character correlation using pairwise comparisons on a phylogeny. J. Theor. Biol. 202, 195–204.
15. Nunn, C.L., and Barton, R.A. (2001). Comparative methods for studying primate adaptation and allometry. Evol. Anthropol. 10, 81–98.
16. Stevens, J.R., Rosati, A.G., Ross, K.R., and Hauser, M.D. (2005). Will travel for food: Spatial discounting in two New World monkeys. Curr. Biol. 15, 1855–1860.
17. Stevens, J.R., Hallinan, E.V., and Hauser, M.D. (2005). The ecology and evolution of patience in two New World monkeys. Biol. Lett. 1, 223–226.
18. Rosati, A.G., Stevens, J.R., Hare, B., and Hauser, M.D. (2007). The evolutionary origins of human patience: Temporal preferences in chimpanzees, bonobos, and human adults. Curr. Biol. 17, 1663–1668.
19. Bond, A.B., Kamil, A.C., and Balda, R.P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica). J. Comp. Psychol. 121, 372–379.
20. Bond, A.B., Kamil, A.C., and Balda, R.P. (2003). Social complexity and transitive inference in corvids. Anim. Behav. 65, 479–487.
21. Emery, N.J., and Clayton, N.S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. Science 306, 1903–1907.
22. Deaner, R.O., van Schaik, C.P., and Johnson, V. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. Evol. Psychol. 4, 149–196.
23. de Waal, F.B.M., and Luttrell, L.M. (1989). Toward a comparative socioecology of the genus Macaca: Different dominance styles in rhesus and stumptail macaques. Am. J. Primatol. 19, 83–109.
24. Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. Evol. Anthropol. 16, 224–238.
25. van Schaik, C.P., and van Noordwijk, M.A. (1988). Scramble and contest feeding competition among female long-tailed macaques (Macaca fascicularis). Behaviour 105, 77–98.
26. Fragaszy, D.M., Fedigan, L.M., and Visalberghi, E. (2004). The Complete Capuchin: The Biology of the Genus Cebus (New York: Cambridge University Press).
27. Anderson, J.R. (1996). Chimpanzees and capuchin monkeys: Comparative cognition. In Reaching Into Thought: The Minds of the Great Apes, A.E. Russon, K.A. Bard, and S.T. Parker, eds. (Cambridge: Cambridge University Press), pp. 23–56.
28. de Waal, F.B.M., and Johanowicz, D.L. (1993). Modification of reconciliation behavior through social experience: An experiment with two macaque species. Child Dev. 64, 897–908.
29. Barth, J., and Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (Pan troglodytes, Pan paniscus, Gorilla gorilla, and Pongo pygmaeus) and young children (Homo sapiens). J. Exp. Psychol. Anim. Behav. Process. 32, 239–252.
30. Vlamings, P. (2006). Inhibition in great apes: Performance on a detour-reaching and reversed contingency task. Master thesis, University of Maastricht, Maastricht, the Netherlands.
31. Piaget, J. (1954). The Construction of Reality in the Child (New York: Basic Books).
32. Call, J. (2001). Object permanence in orangutans (Pongo pygmaeus), chimpanzees (Pan troglodytes), and children (Homo sapiens). J. Comp. Psychol. 115, 159–171.
33. Rosati, A.G., Stevens, J.R., and Hauser, M.D. (2006). The effect of handling time on temporal discounting in two New World primates. Anim. Behav. 71, 1379–1387.
34. Cohen, J., and Cohen, P. (1983). Applied Multiple Regression/Correlation Analysis for the Behavioral Sciences (New Jersey: Lawrence Erlbaum Associates Inc).