Animal Behaviour 85 (2013) 195–202

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Repeated innovation in great apes

Héctor Marín Manrique [a,*], Christoph J. Völter [a,b], Josep Call [a]

[a] Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[b] Department of Animal Behaviour, University of Bielefeld, Bielefeld, Germany

A R T I C L E I N F O

Article history:
Received 9 August 2012
Initial acceptance 12 September 2012
Final acceptance 17 October 2012
Available online 22 November 2012
MS. number: 12-00617R

Keywords:
cognitive flexibility
great ape
inhibitory control
innovation
primates
prior knowledge
problem solving
puzzle box

Innovation has been defined as a solution to a novel problem or a novel solution to an old problem. The second part of this definition requires the inhibition of previously learnt solution strategies before a novel solution can be found. Therefore, inventing novel solutions for an old problem is considered to be particularly difficult. We investigated the ability of great apes to produce multiple new solutions to a task after each of those solutions became obsolete. We presented all four nonhuman great ape species with a task consisting of extracting a food reward from a puzzle box. Initially, the task could be solved in three different ways that varied in difficulty. After subjects discovered the first solution, we allowed them to use it for some trials and then it became obsolete. If the apes could overcome their initial response and find the next solution, we again allowed them to use it for some time and once again it became obsolete. The final step consisted of finding the third solution to secure the food reward. We found that all species except orang-utans, *Pongo abelii*, were able to solve all versions of the problem. Furthermore, they overcame the obsolete techniques quickly and efficiently, indicating high degrees of behavioural flexibility and inhibitory control. In contrast to previous research on social learning, our results suggest that great apes are not conservative and adjust their behaviour flexibly when the physical constraints of a task change.

Prior knowledge plays a fundamental role in innovative problem solving (e.g. Köhler 1925; Epstein et al. 1984). According to Epstein's (1999, page 759) generativity theory novel behaviours or ideas are the 'result of an orderly and dynamic competition among previously established behaviours, during which old behaviours blend or become interconnected in new ways'. This account explicitly highlights the importance of previous experience in order to generate genuinely novel strategies. On the one hand, such previous experience might involve shaped behaviours that lead to novel solutions by an automatic chaining process (Epstein et al. 1984, Epstein 1987). On the other hand, general (i.e. not directly reinforced) experience with objects and their structural properties can be beneficial for solving problems. For instance, Birch (1945) showed that chimpanzees, *Pan troglodytes*, who had a chance to explore an object during free play outperformed subjects without such previous experience in a subsequent test that required the manipulation of that particular object. Whereas chaining can only produce novel solutions on the basis of previously learnt associations, the latter type of knowledge might involve the encoding of structural relations, which enables the subject to adjust its behaviour more flexibly to the task demands (Wertheimer 1959).

* Correspondence: H. M. Manrique, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
E-mail address: hector_manrique@eva.mpg.de (H. M. Manrique).

Prior knowledge, however, may not always have a positive effect on innovative problem solving; it can also produce mental blockages in the form of Einstellung effects (Luchins & Luchins 1959) or functional fixedness (Duncker & Lees 1945). Recently, Hanus et al. (2011) reported evidence consistent with functional fixedness in chimpanzees in the floating peanut task. In this task, subjects are confronted with an out-of-reach peanut located at the bottom of a vertically oriented tube. The solution to this problem consists of pouring water inside the tube to lift the (floating) peanut off the bottom to get access to it once it reaches the tube opening. Hanus et al. (2011) found that the solution to this problem was facilitated by the introduction of a novel water dispenser. Hanus et al. argued that this may have been caused by the old dispenser having a fixed function (gained by past experience) of supplying drinking water, which would hinder the invention of the novel usage of water. On a more general level, solving a task in one way may hinder the invention of other solutions. Several studies reported such conservatism in chimpanzees in the social-learning domain (Marshall-Pescini & Whiten 2008; Hrubesch et al. 2009; Gruber et al. 2011): once acquired, chimpanzees stayed with their initial solution even though they received repeated demonstration of a more efficient solution. However, it is unclear to what extent this conservatism would also apply when the task constrains change, thus rendering the initial solution obsolete.

Currently, an unresolved question is, what determines the usefulness of prior knowledge? Why does prior knowledge

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2012.10.026

sometimes help innovation whereas at other times it blocks innovation in problem solving? Innovation has been defined as ‘a solution to a novel problem, or a novel solution to an old one’ (Kummer & Goodall 1985, page 203). The first part of this definition might be very different from a cognitive point of view to the second part. Finding a solution to a novel problem often includes applying a previously used solving strategy (or at least parts of it) to the novel problem (transfer task). Therefore, motor routines and/or functional relations gained by previous experience might remain the same. In contrast, finding a new solution to an old problem might require first the inhibition of the old strategy including learnt motor routines and functions of relevant objects such as tools (functional fixedness) before a new solution can be found (inhibition task). Therefore, prior knowledge might facilitate transfer tasks but hinder inhibition tasks. A task that requires subjects to adopt new solutions repeatedly to cope with changing demands, while inhibiting the use of previously successful solutions, appears to be particularly difficult.

In humans and monkeys the associative brain areas, in particular the prefrontal cortex, have been related to executive functions and inhibitory control (Miller & Cohen 2001). However, not all great ape species seem to be equivalent in inhibiting prepotent responses and producing novel, creative solutions. In a detour-reaching task requiring subjects to avoid reaching directly for the food reward, orang-utans, *Pongo abelii*, outperformed chimpanzees, bonobos, *Pan paniscus*, gorillas, *Gorilla gorilla*, and 3–5-year-old human children suggesting superior inhibitory control in orang-utans (Vlamings et al. 2010). Gorillas performed worse than the other great apes on a battery of inhibitory control tasks (Amici et al. 2008). However, such differences have not been detected in other tasks with a strong inhibitory component such as the reverse reward contingency task (Boysen & Berntson 1995; Vlamings et al. 2006; Uher & Call 2008).

Innovation rates have also been positively correlated with the volume of associative brain areas (isocortex and striatum in primates, hyperstriatum ventrale and neostriatum in birds; Lefebvre et al. 2004). Among primates, great apes (especially chimpanzees and orang-utans) show both the highest innovation rates and the largest relative brain size in associative areas. Few studies, however, have investigated innovation from a comparative perspective. One such study has recently been reported by Auersperg et al. (2011): they presented keas, *Nestor notabilis*, and New Caledonian crows, *Corvus moneduloides*, with a puzzle box that initially offered four different options to extract a food reward. Once they mastered one solution that particular solution was blocked. Thus, the birds repeatedly had to abandon a previously used technique to find a new solution. Auersperg et al. found that one (of six) keas and one (of five) crows invented all four solutions, showing significant flexibility in problem solving across these two species of birds.

Orang-utans, chimpanzees and children, unlike gorillas, have been shown to use water as a tool in the floating peanut task (Mendes et al. 2007; Hanus et al. 2011). Orang-utans also outperformed chimpanzees and bonobos in a task that required them to use the shaft of an electrical cable as a straw to extract fruit juice from a container (Manrique & Call 2011). However, there have been no experimental analyses of differences between the four nonhuman ape species with regard to their innovativeness, especially when coping with multiple changes in the apparatus.

The goal of the present study was to investigate the ability of the great apes to produce multiple new solutions to a task after each of those solutions became obsolete. This means that this study assessed not only whether species varied in their ability to produce new responses to meet new task demands but also their ability to refrain from using responses that no longer worked. We presented all four ape species with a task consisting of extracting a food reward from a puzzle box. Initially, the task could be solved in three different ways that varied in complexity. After subjects discovered the first (easiest) solution, we allowed them to use it for some trials and then it became ineffective. If the apes could overcome their initial response and find the next solution, we allowed them to use it for some time and once again we rendered it obsolete. The final step consisted of finding the third (and final) solution to secure the food reward. Based on the high innovation rates of great apes in the wild compared to other primates (Reader & Laland 2002) we expected significant flexibility and innovation in great apes’ problem solving, that is, efficient adjustments in behaviour when the physical constraints of the tasks were changed. Moreover, based on their high innovation and inhibition rates from past studies we expected orang-utans to outperform the other species.

METHODS

Subjects

Five chimpanzees, five bonobos, three gorillas and seven orang-utans housed at the Wolfgang Köhler Primate Research Centre (WKPRC) in the Leipzig Zoo participated in this study (see Table 1). There were six males and 14 females ranging in age from 3 to 35 years. Thirteen subjects were mother-reared and seven nursery-reared. Subjects were housed in social groups of 6–18 individuals and spent the day in indoor (175–430 m^2) or outdoor (1400–4000 m^2) enclosures, depending on the season. Both enclosures were spacious and equipped with climbing structures, natural vegetation and enrichment devices to foster extractive foraging activity that included the use of tools. Subjects were individually tested (the only exception being mothers with their dependent offspring) in special test cages (5.1–7.3 m^2) interconnected by lockable doors. The apes were allowed to decide whether to participate or not in our tests. Subjects were not deprived of food. They were provided with fresh fruits, vegetables, eggs, cereals, leaves and meat (once a week) distributed in three main meals (0730, 1330 and 1700 hours). Some more food was dispensed between 0730 and 1330 hours (mainly fresh fruit) and at 1730 hours, as part of the enrichment programme. Water was available ad libitum during testing. The study complied with the European and World Associations of Zoos and Aquariums (EAZA

Table 1
Subjects that participated in the study

Subject	Species	Sex	Age (years)	Rearing history
Fifi	Chimpanzee	Female	16	Mother
Alexandra	Chimpanzee	Female	9	Nursery
Alex	Chimpanzee	Male	8	Nursery
Jahaga	Chimpanzee	Female	16	Mother
Trudi	Chimpanzee	Female	16	Mother
Joey	Bonobo	Male	26	Nursery
Kuno	Bonobo	Male	12	Nursery
Limbuko	Bonobo	Male	13	Nursery
Yasa	Bonobo	Female	11	Mother
Ulindi	Bonobo	Female	15	Mother
Dokana	Orang-utan	Female	18	Mother
Dunja	Orang-utan	Female	35	Nursery
Padana	Orang-utan	Female	11	Mother
Pini	Orang-utan	Female	20	Mother
Bimbo	Orang-utan	Male	28	Nursery
Kila	Orang-utan	Female	8	Mother
Raja	Orang-utan	Female	6	Mother
Kibara	Gorilla	Female	5	Mother
Viringika	Gorilla	Female	14	Mother
Louna	Gorilla	Female	3	Mother