

A sex difference in effect of prior experience on object-mediated problem-solving in gibbons

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Abstract Understanding the functionally relevant properties of objects is likely facilitated by learning with a critical role for past experience. However, current evidence is conflicting regarding the effect of prior object exposure on acquisition of object manipulation skills. This may be due to the influence of life history variables on the capacity to benefit from such experience. This study assessed effect of task-relevant object exposure on object-mediated problem-solving in 22 gibbons using a raking-in task. Despite not using tools habitually, 14 gibbons spontaneously used a rake to obtain a reward. Having prior experience with the rake in an unrewarded context did not improve learning efficiency in males. However, females benefitted significantly from the opportunity to interact with the rake before testing, with reduced latencies to solution compared to those with no previous exposure. These results reflect potential sex differences in approach to novelty that moderate the possible benefits of prior experience. Due to their relatively high energetic requirements, reproductively active females may be highly motivated to explore potential resources; however, increased investment in developing offspring could make them more guarded in their investigations. Previous

exposure that allows females to learn of an object's neutrality can offset this cautious exploration.

Keywords Gibbons · Object experience · Problem-solving · Sex differences

Introduction

Understanding the functional properties of objects that make them useful in novel situations is likely facilitated by prior exposure during which object affordances can be investigated (Kummer and Goodall 1985). However, explorations of the effect of previous object experience on object-mediated problem-solving have provided conflicting results. Birch (1945) tested six captive chimpanzees (*Pan sp.*) on a raking-in task. On first exposure, only one ape purposefully used the tool (a stick) to draw in an out-of-reach food item. The chimpanzees were then given free access to sticks in their home enclosure for 3 days, following which they were tested again on the rake problem. This time all chimpanzees obtained the food within 20 s, leading Birch to conclude that these apes came to perceive the functional relationship between tool, reward and themselves only after experiencing it as a potential extension of the arm. Such experience has been shown to induce neural reorganisation in the macaque (*Macaca fuscata*) cortex that results in the 'tool' potentially becoming incorporated into the body schema, facilitating directed manipulation, suggesting similar neural restructuring may occur in the ape brain when stimulated appropriately (Obayashi et al. 2002; Hihara et al. 2006). However, Brent et al. (1995), using a similar raking-in paradigm with chimpanzees differing in levels of previous object exposure, reported no difference in performance between

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object-experienced and inexperienced groups, indicating exposure alone may be insufficient to induce the formation of novel neuronal connections.

Object knowledge did affect performance on novel problem-solving tasks in cotton-top tamarins (*Saguinus oedipus*), a species that do not habitually use tools (Hauser et al. 2002). Tasks included using objects to draw in out-of-reach food items with subjects presented with a functional versus non-functional tool (based on size, shape, materials or tool-goal layout) choice on each trial. After an initial training phase, individuals experienced at using objects to solve problems (having participated in previous means-end object use studies) learned novel object-as-rake problems significantly faster than individuals with no such experience although understanding of what makes an object functionally relevant did not differ markedly between groups. Hauser and colleagues suggest that this is because tamarins possess an evolved cognitive mechanism for processing object properties. The role of prior experience is to somehow prime these mechanisms to attend to more task-relevant features thus expediting acquisition of the correct behavioural response.

In a follow-up study, Spaulding and Hauser (2004) revisited the hypothesis that tamarins are equipped with an innate mechanism for understanding the properties of objects. Using the same paradigm, tool-naïve callitrichids did not demonstrate spontaneous understanding of the functional significance of objects as tools, questioning the presence of an evolved processing mechanism. Two closely related species were tested, *S. oedipus* (cotton-top tamarin) and *Callithrix jacchus* (common marmoset) with the latter learning to discriminate functionally correct tools more quickly. Although these results force a rejection of a domain-specific cognitive module for understanding the relevant features of objects that make them useful in these species (although Spaulding and Hauser suggest a modification to an innate mechanism that understands object mechanics more generally rather than in a tool-using context), that there are significant species differences implicates a role for environmental factors in the development of object-mediated problem-solving skills. Although these species display many similarities in physiology and life history variables, they differ in foraging techniques with the common marmoset being a gum specialist in contrast to the mainly insectivorous diet of tamarins (Stevens et al. 2005). Gummivory is suggested to have selected for patience as there is a delay between accessing the resource through scratching at the tree bark and the flow of sap (Stevens et al. 2005). In the task setup, this may give marmosets an advantage in that they are less impulsive when faced with a potential food source allowing subjects to examine the options before making a choice.

Previous opportunity to explore objects and their properties could manifest as increased propensity to approach and interact with novel objects (a requirement for successful object-mediated solutions), and improved efficiency in goal-directed manipulation. Here, we examine the effect of prior domain-specific experience on acquisition of object manipulation skills in gibbons (Hylobatidae), a much understudied group of apes, particularly with reference to their cognitive abilities. These small arboreal apes primarily live in monogamous pairs with their associated offspring and are characterised by limited sexual dimorphism, complex vocal duets between the male and female bonded pair and brachiating mode of locomotion (Cunningham and Mootnick 2009). Current data suggest that gibbons do not frequently use objects for resource acquisition; therefore, it is unlikely that they possess any evolved cognitive mechanism specifically for processing object affordances. Instead, understanding the functionally relevant features of objects is likely to come about through learning, with an important role for previous experience. However, potential benefits gained from prior exposure to objects may be linked to ecological and life history variables, such as habitat, age and sex (Kummer and Goodall 1985; Lee 1991). Gibbons are large-brained primates (Cunningham and Mootnick 2009) and as such are expected to have the cognitive capacity to learn about object affordances. Prior exposure to a potential ‘tool’ before using to obtain a reward is expected to increase efficiency in goal realisation; however, the degree of benefit may be moderated by associated costs that will vary according to sex and developmental stage.

Methods

Subjects were 22 gibbons (age 4–30 years) housed at the Gibbon Conservation Center (GCC), California. Representatives from all four genera were included in the sample (Table 1), none of which had taken part in cognitive experiments requiring object manipulation previously. It was therefore assumed that their experience of objects was limited to those provided in their enclosure (see below). Gibbons were housed in outdoor enclosures $10 \times 3 \times 4$ m, with a secondary area $4 \times 3 \times 2.5$ m that was generally available at all times but could be closed off to separate individuals as required. All cages were a minimum of 5.5 m apart and visual barriers in the form of solid tarpaulins and planted vegetation obstructed direct views between adjacent enclosures, although gibbons were in auditory contact with neighbouring groups. Each enclosure was furnished with an insulated shelter for sleeping, floor-level feeding platforms or raised feeding containers, ropes and branches (see Mootnick 1997a for more details of enclosure design). The feeding regime at GCC varied with season and was tailored

to individual gibbons. Generally, the gibbons were fed four times a day, beginning with breakfast of fruits and primate biscuits, a main feed of fruits and vegetables and two further feeds of apples, bananas and greens (Mootnick 1997b). A proportion of food was handed to individuals; the design of enclosures allowed gibbons to extend their arms through the fencing to accept food from caregivers. Water was available ad libitum.

The task involved pulling in a rake-shaped object (tool) to obtain a food reward (N.B. Although this cannot be considered true tool-use (Fragaszy et al. 2004), the rake will hereafter be referred to as a tool for ease of literacy). A wooden table (110 × 27 × 12 cm) was placed outside the main enclosure adjacent to the gibbons' feeding platform. For the *Hylobates* subjects, this required the elevation of the apparatus to a height corresponding to the feeding container approximately 1 m from the enclosure floor. These subjects were uneasy about descending to floor level, so the table was placed on scaffolding at the required height. All other subjects were routinely fed at floor level and were not adverse to spending significant amounts of time there. Although this is not natural behaviour for wild gibbons, it is common in captive animals. The table had a

2-cm lip along three edges (not the edge aligned with the cage) to prevent the rake and food item sliding off. The rake consisted of an aluminium rectangle (25 × 12 cm) fixed to one end of a 115-cm handle with the free end protruding through the chain link fence approximately 5 cm into the enclosure (Fig. 1). This elevated the end of the rake to facilitate grasping by the gibbons' elongated hands (see Beck (1967) for a similar arrangement with a string pulling task).

Subjects were divided into two groups, no prior exposure (NE; $N = 11$) and prior exposure (PE; $N = 10$). The PE group was exposed to the apparatus in situ for 7 days immediately preceding testing. The table and rake were placed as they would be during the test situation, although no reward was used. The tool could be manipulated in its location; however, the plate attached to the end prevented it being pulled completely into the enclosure. Each morning, the rake was reset onto the table in its original starting position if necessary. No other interaction with the apparatus by the experimenter occurred. The NE group was exposed to the rake for the first time on presentation of the test trial.

The gibbons were free to move about their enclosure throughout the trials. As they were frequently distracted

Table 1 Subjects by genus, species, sex, age, experimental group and housing type

Subject	Genus	Species	Sex	Age (years)	Group	Housing	Reached solution
Maung	<i>Hoolock</i>	<i>hoolock</i>	M	4	NE	Solitary	Success
Chester	<i>Hoolock</i>	<i>hoolock</i>	M	5	NE	M/F pair	Success
Betty	<i>Hoolock</i>	<i>hoolock</i>	F	5	PE	M/F pair	Success
Arthur	<i>Hoolock</i>	<i>hoolock</i>	M	9	PE	M/F pair	Success
Sasha	<i>Nomascus</i>	<i>leucogenys</i>	M	27	PE	Solitary	Success
Ricky	<i>Nomascus</i>	<i>leucogenys</i>	F	15	NE	Family group	Success
Vok	<i>Nomascus</i>	<i>leucogenys</i>	M	17	NE	Family group	Success
Kino	<i>Symphalangus</i>	<i>syndactylus</i>	M	20	NE	Solitary	Success
Dudlee	<i>Symphalangus</i>	<i>syndactylus</i>	F	9	PE	F/F sib pair	Success
Kimbo	<i>Symphalangus</i>	<i>syndactylus</i>	F	5	PE	F/F sib pair	Success
Chloe	<i>Hylobates</i>	<i>moloch</i>	F	13	NE	Family group	Success
Ivan	<i>Hylobates</i>	<i>moloch</i>	M	30	PE	Solitary	Failure
Chillibi	<i>Hylobates</i>	<i>moloch</i>	M	16	PE	Solitary	Failure
Khusus	<i>Hylobates</i>	<i>moloch</i>	F	9	NE	Family group	Success ^a
Tuk	<i>Hylobates</i>	<i>pileatus</i>	F	12	PE	Solitary	Success
Valentina	<i>Hylobates</i>	<i>pileatus</i>	F	7	PE	Family group	Success
Birute	<i>Hylobates</i>	<i>pileatus</i>	M	22	NE	Family group	Failure
JR	<i>Hylobates</i>	<i>pileatus</i>	F	15	NE	Family group	Failure
Kanako	<i>Hylobates</i>	<i>pileatus</i>	F	4	NE	Family group	Failure
Ruby	<i>Hylobates</i>	<i>agilis</i>	F	18	NE	Mother/infant	Failure
Bebop	<i>Hylobates</i>	<i>agilis</i>	M	15	PE	Father/daughter	Failure
Lilleth	<i>Hylobates</i>	<i>agilis</i>	F	4	PE	Father/daughter	Failure

NE no prior exposure, PE prior exposure

^a Individual excluded due to method of obtaining reward



Fig. 1 Female pileated gibbon (*Hylobates pileatus*) using rake tool to obtain food reward

from the task by disturbances or vocalisations in other enclosures, an area of 1.5 m² around the apparatus was designated as the “target area”. Only ‘time in target area attending to the task’ was considered time available for solution. If the ape was within the target area but facing away from the apparatus or was engaged in non-task-related behaviour, this time was subtracted from the overall ‘in target area’ time. Some gibbons became distressed if separated for testing; these individuals were therefore tested with their family groups. In these cases ($N = 10$), data were initially recorded for all apes in the enclosure. When one learned to use the tool, behavioural recording of the unsuccessful gibbons was discontinued and only the individual that had obtained the reward was considered. This was possible as when one individual learned the task, they monopolised access to the tool with remaining occupants being tolerated in close proximity. Three pairs were separated during test trials, with their mate being isolated in the adjacent enclosure and both partners being tested. There was a possibility that the individual not being tested had visual access to their partner performing the task (although this would have been limited due to placement of the apparatus) and so may have learned task-relevant knowledge. In two of the three pairs, time to solution varied notably; however, in both cases, it was the second to be tested that showed longer latencies (*Pair 1*: First tested time to solution = 38s, second tested = 81s; *Pair 2*: First tested time to solution = 46s, second tested = 168s). The final pair differed in time to solution by only 12 s. Order effects were therefore assumed negligible. The remaining individuals ($N = 6$) were individually housed.

For testing, a reward (raisin or grape) was placed, in view of the subject, on the end of the table beyond direct reach, between the subject and the end-plate of the rake. Gibbons were given 30 min to obtain the food. Times taken to obtain the reward and latency to first physical contact with the rake by hand, foot or mouth were recorded, along with the number of goal-oriented actions prior to solution. The latter are not included in analyses as there was a significant correlation between latency to solve and number of directed actions (Pearson’s: $r = 0.874$, $P < 0.001$, $N = 13$).

All data were checked for normality and log-transformed where necessary. Independent samples t-tests were used to compare time to solution and latency to first physical contact between NE and PE groups, for those apes that reached solution and for the sample as a whole. When analysing time to first physical contact for all individuals, regardless of whether they reached solution or not, three gibbons (*Hylobates moloch* ($N = 1$), *H. pileatus* ($N = 1$), *H. agilis* ($N = 1$)) were excluded as they failed to interact with the apparatus throughout the exposure time. Genera differences were analysed using 2-way ANOVA. Age differences between apes that reached solution and those that did not and between the NE and PE groups were investigated using independent samples t-tests. In addition, distribution of age classes within these groups was analysed. Gibbons were categorised according to age classifications described in Palombit (1994) (Infants <1 year; Juvenile 1–3 years; Adolescent 3–5 years; Sub-adult 6–8 years; Adult 8 years+). Chi-square tests assessed whether the distribution of age classes differed between groups. Alpha was set at 0.05, and all tests were 2-tailed.

Results

Of 22 gibbons tested, 14 reached solution within the 30-min exposure period. One PE female (*H. moloch*) was excluded because she obtained the reward fortuitously by bouncing on the handle, causing vibrations that moved the food within reach. Prior exposure to the rake did not influence the likelihood of solving the task: 7/11 and 6/10 gibbons obtained the reward in NE and PE groups, respectively. Time available for solution did not affect the outcome as there was no significant difference in time spent in the target area between solvers and non-solvers (Solution mean = 87.08s (SE = 15.959); No solution mean = 99.13s (SE = 22.414), $t(19) = 0.505$, $P = 0.619$). In the apes that solved the task, time taken did not differ between groups (NE mean = 108.83s (SE = 32.843); PE mean = 72.71s (SE = 12.950), $t(11) = 0.490$, $p = 0.639$), nor did latency to first contact (NE mean = 33.00s (SE = 13.224); PE mean = 48.29s (SE = 20.729), $t(11) = 0.232$, $P = 0.821$).

Overall time in target area did not differ between NE and PE groups (NE mean = 92.36s (SE = 18.907); PE mean = 90.90s (SE = 18.028), $t(19) = 0.457$, $P = 0.653$); prior exposure to the apparatus did not influence time engaged with the task. Latency to first contact with the rake was not significantly different between NE and PE groups when all individuals that manipulated the object during the exposure time (3 *Hylobates* did not) were included (NE mean = 26.56s (SE = 9.221); PE mean = 50.44s (SE = 16.281), $t(16) = 1.300$, $P = 0.212$).

Surprisingly, gender interacted with prior exposure: PE females required less time to solution than their NE counterparts (NE mean = 194.00s (SE = 26.00); PE mean = 67.50s (SE = 18.50); $F(1,5) = 7.298$, $P = 0.043$) (Figure 2). No significant difference was found for males in time to solution (NE mean = 66.25s (SE = 27.762); PE mean = 67.50s (SE = 18.50), $F(1,4) = 0.125$, $P = 0.742$) (Fig. 2). Time to first tool contact did not differ for either gender (Females: NE mean = 18.50s (SE = 12.50); PE mean = 16.80s (SE = 5.774), $F(1,5) = 0.014$, $P = 0.911$. Males: NE mean = 40.25s (SE = 18.821); PE mean = 127.00s (SE = 4.00); $F(1,4) = 5.002$, $P = 0.089$), although males with prior experience took notably longer to contact the rake (Fig. 2). This result became significant when looking at all males tested regardless of whether they reached solution or not; males that were exposed to the apparatus before testing showed longer latencies to contact the object than those for whom the apparatus was novel (NE mean = 36.60s (SE = 15.029); PE mean = 112.33s (SE = 14.847), $F(1,8) = 8.654$, $P = 0.026$).

The NE and PE groups were of similar mean age (NE mean = 13.73 years (SE = 2.00); PE mean = 13.20 years (SE = 2.867), $t(19) = 0.028$, $P = 0.978$), and each group contained an equal distribution of age classes ($\chi^2(2) = 0.148$, $P = 0.104$). The mean age of gibbons that reached

solution was 11.38 years (SE = 1.917); this did not differ significantly from the mean age non-solvers (mean = 15.50 years (SE = 3.059) ($t(19) = 0.934$, $P = 0.362$). As before, distribution of age classes within these groups did not differ ($\chi^2(2) = 4.523$, $P = 0.928$).

In those apes that reached solution, there was no significant difference in time to solution across genera ($F(3,5) = 1.30$, $P = 0.371$). Group (NE or PE) also remained non-significant ($F(1,5) = 1.381$, $P = 0.293$); however, *Hoolock* subjects did obtain the reward in a shorter time (*Hoolock*; mean = 57.25s (SE = 13.708); *Nomascus*; mean = 87.67s (SE = 40.176); *Symphalangus*; mean = 89.00s (SE = 32.005); *Hylobates*; mean = 134.33s (SE = 50.551)). Latency to first physical contact again revealed no significant differences between genera ($F(3,5) = 1.317$, $P = 0.217$).

Discussion

The effects of prior object-relevant experience varied between sexes. For males, previous exposure did not increase the likelihood of successful object use to obtain a reward. In contrast, females exhibited a significant decrease in time to solution with previous experience. While sample size makes conclusions tentative, females appear cautious in their initial responses to a novel object. However, this can be offset by prior exposure to that object enabling them to learn first hand of its neutrality, provided they are taking the opportunity to interact with the apparatus in the prior exposure period. From these data, it is not known how much time individuals spent manipulating the tool object before the test phase; although they have the opportunity to learn, it cannot be certain that they did interact in a way that would promote understanding of the rake's properties and so its potential as a tool. Having said this, the data do support gender-specific effects of having access to the objects beforehand. This may be the result of increased manipulation by females in the prior exposure period compared to males which would account for such experience having increased benefits for the former, or because innate female neophobic tendencies are being overridden by experience.

The propensity of object-naïve females to take longer to obtain the reward contrasts with their overall shorter latencies to first contact with the rake. These patterns may reflect differences in cognitive processing driven by life history variables. Females may be more motivated to explore potential novel food sources due their relatively high energetic requirements (Lee 1991). This is supported by evidence of greater tool-use proclivity and proficiency for extracting high-quality food items in female great apes (Boesch and Boesch 1981; Lonsdorf 2005). However, when

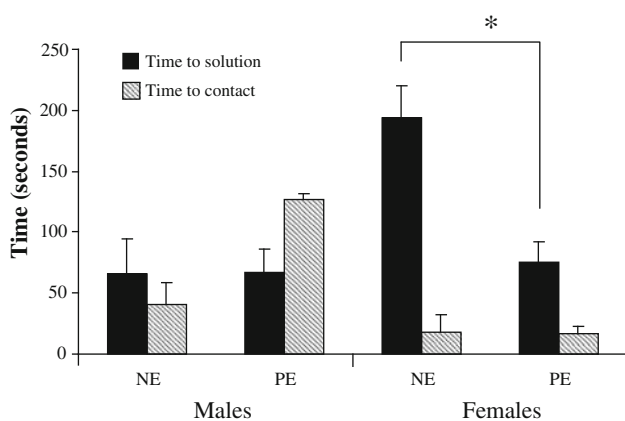


Fig. 2 Mean (+1SE) time to solution and mean latency (+1SE) to first physical contact in those apes that reached solution by gender (* = $P < 0.05$)

faced with a potential source of risk such as a novel object, females appear more guarded in their initial manipulations. This may be because they have more to lose in fitness terms should they be pregnant or with dependent offspring.

That females are more risk averse when encountering novel situations is also supported by evidence from an exhaustive survey of innovative behaviour in primates by Reader and Laland (2001). Innovation often requires investigation of novel objects and environments that although have the potential to provide benefits such as access to new foods or more efficient use of existing resources, also present significant risks in terms of increased susceptibility to predation, energetic expenditure or exposure to hazardous food sources. Here, males were seen to be responsible for more innovation given their relative proportions in the population, suggesting females are balancing costs and benefits, potentially through more cautious interactions with novelty resulting in fewer instances of emerging innovation.

As males have fewer reproductive constraints, they do not display the same responses to potential risks. In this study, males approached the apparatus quickly in both conditions with prior exposure having no effect on time to solution. There was, however, an increase in time to first contact; the unbaited apparatus presented to the PE group offered no incentive, and so generalisation of the perceived non-interest in object manipulation may account for their initial delay in manipulating the rake in the test session.

Age did not influence performance in either group, counter to traditional expectations that younger individuals are more likely to explore and manipulate novel objects, possibly due to parental protection providing safe conditions for investigation (Kummer and Goodall 1985). Age differences in object exploration and successful application to problem-solving have been reported (Reader and Laland 2001; Kendal et al. 2005), although suggesting an association between maturity and understanding of object affordances rather than in the expected direction. Experience is likely confounded with age, as older individuals are likely to have had more opportunities to learn; however, this does not preclude the expectation of greater propensity for exploration and manipulation in younger individuals. What may be paramount is exposure to objects during a sensitive developmental window. Menzel et al. (1970) reported that restriction rearing resulted in reduced object manipulation skills in chimpanzees. More recently, enculturated chimpanzees (raised with extensive exposure to human artefacts and behaviours) were shown to be better tool-users than semi-enculturated apes (Furlong et al. 2008), again suggesting exposure to objects during development enhances proficiency in goal-directed object use in later life. The gibbons in this study were relatively naïve in terms of object experience with, to our knowledge, no enhanced

exposure to artefacts during development. Exposure for the 7 days preceding testing may have been insufficient to positively impact upon object use skills in males; earlier or longer learning about object affordances may be important. In addition, the simplicity of the task may have limited the potential benefits gained by previous experience with the rake; tasks with increased levels of complexity may become easier with prior exposure to the objects involved.

Performance across the four genera did not differ; however, hoolock gibbons (*H. hoolock*) showed decreased latencies to obtain the reward compared to the other genera. This is consistent with findings from Cunningham et al. (2006) where these gibbons performed significantly better than all other species tested with performances comparable to (and marginally better than) chimpanzees in a repeated trial raking-in task (Povinelli and Reaux 2000). The reason for the improved performance by hoolocks is unclear although it is worthy of note that the range of this species extends significantly beyond the tropics (Mootnick et al. 1987), suggesting they potentially experience considerable variation in resource abundance that may facilitate greater propensity for environmental exploration.

Longitudinal studies are needed to disentangle the effects of age, sex and experience on development of goal-directed object use. In particular, further investigations of how the level of interaction with potential tools in the period before testing is needed. However, a straightforward relationship between these variables appears unlikely to emerge. Individuals at different life stages may respond to novel objects in different ways dependent on the potential costs and benefits incurred by such exploration. The results presented here suggest that gibbons can learn to manipulate objects to gain a reward. There is some indication that prior exposure improves efficiency of learning and may allow females to overcome initial caution regarding novel objects, thus facilitating successful exploitation of a new resource. The interaction between age, sex and experience with objects warrants further investigation.

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Ethical note This study was carried out in accordance with the ethical policies of the University of Stirling and the Gibbon Conservation Center and in compliance with the current laws governing non-invasive animal research of both the UK and USA.

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