

What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles?

Tecwyn, Emma; Thorpe, Susannah; Chappell, Jackie

DOI:

[10.1007/s10071-011-0438-x](https://doi.org/10.1007/s10071-011-0438-x)

Document Version

Peer reviewed version

Citation for published version (Harvard):

Tecwyn, E, Thorpe, S & Chappell, J 2012, 'What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles?', *Animal Cognition*, vol. 15, no. 1, pp. 121. <https://doi.org/10.1007/s10071-011-0438-x>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

A definitive version was subsequently published in *Animal Cognition* January 2012, Volume 15, Issue 1, pp 121-133 DOI: <http://dx.doi.org/10.1007/s10071-011-0438-x>. The final publication is available at link.springer.com.

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles?

Emma C Tecwyn*, Susannah KS Thorpe[#], Jackie Chappell[#]

Original source published as:

Tecwyn, E. C., Thorpe, S. K. S. and Chappell, J. (2012). What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles? *Animal Cognition* **15**, 121-133. DOI: 10.1007/s10071-011-0438-x

The original publication is available at: <http://link.springer.com/article/10.1007%2Fs10071-011-0438-x>

School of Biosciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK.

*Author for correspondence (ect255@bham.ac.uk)

[#] Joint senior authors

Abstract

We presented three Bornean orangutans with 64 trial-unique configurations of a puzzle-tube to investigate whether they were able to consider multiple obstacles in a path when attempting to retrieve a reward. We were particularly interested in *how* subjects attempted to solve the task, namely which cognitive strategies they could have been using, as this is how we may begin to elucidate the cognitive mechanisms underpinning their behavioural choices. Mental simulation of potential courses of action and their outcomes prior to implementing behaviour is one way in which novel problems may be approached, and has been posited as a key difference in cognitive ability between great apes and monkeys. However, there are several more parsimonious explanations that need to be eliminated first, such as the use of associative learning, or simple procedural rules. To explore this we simulated task outcomes for the 64 trials based on various procedural rules that subjects may have been using derived from the configuration of different cues. Two of the three subjects solved the task, suggesting that they were able to consider at least some of the obstacles in the puzzle-tube before starting their actions to retrieve the reward. This is impressive compared with the past performances of great apes on similar, arguably less complex tasks. Successful subjects may have been using a rule-combination based on what they deemed to be the most relevant cue (the configuration of the puzzle-tube ends), which may be a cognitively economical strategy compared with mental simulation of each trial.

Keywords: orangutan, great ape, mental simulation, planning, cognitive strategies, trap-tube

Introduction

It has been suggested that the ability to mentally simulate potential courses of action and their outcomes prior to acting may explain the apparent cognitive differences between great apes and monkeys (Byrne 1997). This capacity may even have provided a basis for the evolution of the ‘mentalizing’ abilities required for ‘theory of mind’ *sensu* Premack and Woodruff (1978) which is possessed by humans (Frith and Frith 1999), and arguably some other great apes (see Call and Tomasello 2008 for a review of the evidence for chimpanzees). Subtly different scenarios involving what we term ‘mental simulation’ have variously been called ‘abstract problem representation’ (Byrne 1997), ‘secondary representation’ (Suddendorf and Whiten 2001), ‘mental rehearsal’ (Dunbar et al. 2005) and ‘planning’ (Miyata et al. 2011). Therefore we start by clarifying precisely what we mean, which is the mental simulation of physical actions (rather than social behaviour) for current needs. This is consistent with Miyata and colleagues’ definition of planning as the “internal processes of establishing decisions about multiple steps to reach a goal state, before actually starting one’s actions” (Miyata et al. 2011, pp. 46). To clarify, if we imagine a task with all components perceptually present (e.g. a reward inside a puzzle), then mental simulation would be required to represent (1) the goal state (retrieving the reward), (2) possible actions that might be taken to reach the goal state (different manipulations of the reward within the puzzle), and (3) their outcomes (whether actions would result in the reward being retrieved or lost). It is important to differentiate between this kind of situation and one in which some perceptual components of a task are absent, for example where tools for solving a task are located in one room and the actual task in another, which imposes a delay between performing and action and retrieving a reward and concerns planning for future needs (e.g. Dufour and Sterck 2008; Mulcahy and Call 2006a; Osvath and Osvath 2008). Further examples of animals apparently making provisions for future states include western scrub-jays (*Aphelocoma californica*) caching food for the following day (Raby et al. 2007) and a chimpanzee (*Pan troglodytes*) calmly stockpiling projectiles to throw at zoo visitors during agitated displays several hours

later (Osvath 2009). Our focus is not on whether animals are capable of ‘mental time travel’ or pre-experiencing future states or desires; rather we are interested in the capacity for mental simulation that does not necessarily involve self projection. This form of future thinking without the need for personally envisaging a future event (also called semantic prospection) has been largely overlooked (Raby and Clayton 2009). It should also be noted that mental simulation does not necessarily imply any sort of phenomenal consciousness; that is, the subjective ‘feel’ of an experience (Carruthers 1998).

There is some evidence from wild behaviour to suggest that some animals may be capable of mentally simulating physical actions. For example, both mountain gorillas (*Gorilla beringei beringei*: Byrne et al. 2001) and chimpanzees (Corp and Byrne 2002) have been demonstrated to use hierarchical, multi-stage procedures for processing thistle plants and defended leaves respectively, with the authors suggesting that sequence length may be an appropriate estimate of the complexity of underlying mental processes. Most other evidence is based on anecdotal observations of tool-using behaviour, such as a single chimpanzee that used a ‘tool set’ to extract honey from a bees’ nest (Brewer and McGrew 1990). However, another domain in which the capacity for mental simulation of physical action would be beneficial is that of complex arboreal locomotion, particularly during gap-crossing. Sumatran orangutans (*Pongo abelii*) utilize tree sway, whereby a support is oscillated to cross a gap in the canopy and progress forward (Thorpe and Crompton 2006). This often initially requires the support to be swung in the opposite direction (backwards) to the intended travel direction, in order to reach a sufficient magnitude of oscillation. Chevalier-Skolnikoff et al. (1982) suggest that such behaviour may be indicative of mental simulation prior to acting, as opposed to physical experimentation, as during their focal period individuals always succeeded in making the transfers¹. Bard (1995) also found that complex manipulations were exhibited significantly more frequently during arboreal locomotion than in foraging by young wild orangutans in a study based on Piagetian constructs. The author interpreted these findings as a use of

¹ Chevalier-Skolnikoff et al. (1982) actually use the term ‘insightful solution’ to describe tree sway behaviour, which is problematic for reasons described by Kacelnik (2009)

cognitive abilities to achieve efficient and productive travel. It was also noted that planning was only observed in a locomotor context (out of seven defined contexts during which manipulatory behaviours could potentially occur). This was in the form of selecting an appropriate route to reach a mother who had used tree-sway to cross a gap, which the juveniles were unable to repeat, by two individuals (Bard 1995). It has even been hypothesized that arboreal locomotion may have been a precipitator for self-recognition in the great apes (Povinelli and Cant 1995). The authors suggest that the unique combination of problems faced by a great ape ancestor during the Miocene, specifically an arboreal lifestyle to which it became 'committed' and a large body mass, selected for the evolution of self-conception enabling the planning and successful execution of complex locomotion through the rainforest canopy (Povinelli and Cant 1995).

Relatively few studies have attempted to test the capacity for mental simulation experimentally, and the majority of these have either involved tool-use, which biases against non-tool-using species, or been based on computerized tasks, which requires extensive training. Suddendorf and Whiten (2001) describe experiments conducted by Döhl in the late 1960s in which a chimpanzee was able to successfully complete a multi-stage task involving unlocking a series of transparent boxes with keys, leading to a final box containing a reward. Only by assessing the obligate sequence of stages in advance was the subject able to choose the correct initial key, with the researchers claiming that she was able to successfully evaluate the task up to five steps in advance. Lethmate (1982) adapted Döhl's experimental setting for an orangutan, so that it consisted of a choice-box and four boxes with unique bolting mechanisms that could only be opened with a corresponding key. One of the boxes contained a food reward, a further two contained keys (one of which could be used to open the final box containing the reward) and the fourth was empty. The choice-box contained two keys in separate compartments that each opened one of the two key-containing boxes. Choosing one of the tools from the choice-box simultaneously blocked access to the other tool. The contents of all boxes were visible to the orangutan, enabling it to choose the correct initial key that led, via an intermediate sub-goal, to the box containing the reward. Across 400 trials the orangutan chose the correct initial key significantly more than expected by chance (in 312 trials), and the

average duration of the ‘phase of planning’ before the initial action was 6.5 seconds (Lethmate 1982). More recently, Dunbar et al. (2005) investigated whether allowing chimpanzees, Bornean orangutans (*Pongo pygmaeus*) and children to have a prior view of a puzzle-box before attempting to open it meant that they retrieved a reward inside more quickly than when they were prevented from having a prior view, as the prior view should permit them to consider the nature of the problem and its possible solutions mentally, prior to attempting it. Although there was seemingly an improvement in performance in the prior-view condition, detailed analyses of the data revealed that this was likely a result of experience and learning due to the nature of the experimental design, rather than mental simulation of actions (Dunbar et al. 2005). Further studies have investigated the ability to use tools in a means-means-end sequence (i.e. use a tool to retrieve another tool, which could be used to retrieve a food reward). Gorillas and orangutans were able to use a short tool to reach a longer tool, and only did so when the long tool was needed to reach the reward (Mulcahy et al. 2005). Japanese macaques (*Macaca fuscata*) learned how to sequentially use two tools within 50 trials after extensive training with both short and long tools (Hihara 2003). A similar study with tamarins (*Saguinus oedipus*) found that subjects were only able to succeed at a pulling task involving two tools hooked together (tools were not in spatially distinctive locations due to the species’ limited manual dexterity) after sufficient training (Santos et al. 2005). In recent work on New Caledonian crows (*Corvus moneduloides*) on the other hand, some individuals succeeded at tasks requiring sequential use of 3 tools (Wimpenny et al. 2009). Some authors suggest that certain individuals may even use abstract causal rules in novel contexts (Taylor et al. 2010). Results from experiments with keas (*Nestor notabilis*) in which subjects’ ability to open artificial fruit boxes requiring manipulations in multiple steps was tested suggested that in more complex tasks, permitting a preview period meant that birds were quicker to correct inappropriate actions (Miyata et al 2011). Evidence from studies using computer-based tasks is also indicative of mental simulation during problem-solving in primates and birds. Biro and Matsuzawa (1999) demonstrated that a chimpanzee was able to establish the correct sequence in a numerical ordering task prior to making its first choice. In 2D maze navigation tasks

chimpanzees and capuchins (*Cebus apella*) solved more mazes without error than predicted by chance (Fragaszy et al. 2003). Both species were capable of self-correcting mistakes and making appropriate detours (Fragaszy et al. 2003), though a later study found that capuchins frequently made errors when the correct path meant moving away from the global goal (Fragaszy et al. 2009). A similar study with pigeons (*Columba livia*) found evidence of planning of actions one step (and possibly two steps) in advance in computerized maze tasks (Miyata and Fujita 2008). Finally, in studies of planning behaviour with two bottlenose dolphins (*Tursiops truncatus*), subjects had to learn to reuse a weight as a tool by dropping it into boxes that resulted in a reward being released, but one of the boxes retained the weight so that it could not be reused. Both individuals rapidly learned to visit the weight-retaining box last in order to obtain a maximum reward (Kuczaj et al. 2009).

Fewer studies still have attempted to address *how* tasks that apparently require mental simulation of actions prior to implementing them might be approached by subjects, with regards to alternative behavioural strategies that might be used. Seemingly complex behaviour does not necessarily imply that advanced cognitive processes are actually involved, and there are often several simpler, more parsimonious explanations that need to be eliminated, such as associative learning, or the use of arbitrary cues to form procedural rules. Taylor et al. (2007) claimed that New Caledonian crows in their study solved a sequential tool-use task by using analogical reasoning, but Wimpenny et al. (2009) conducted experiments that suggested simpler processes such as chaining (the interconnection of separate behavioural repertoires, *sensu* Epstein 1984) may be sufficient to explain successful performance.

We designed a puzzle-tube task based on the trap-tube paradigm (Visalberghi and Limongelli 1994) which was designed primarily to investigate causal reasoning, but is also a useful way of testing a subject's ability to mentally simulate the outcomes of different potential actions, with regards to the position of a trap and its impact on the path of a reward. However, unlike the original trap-tube apparatus in which the only obstacle was a single trap at one side, we incorporated multiple obstacles to force

subjects to evaluate the potential effects of all obstacles, and not just the obstacles closest to the reward. This relates back to Miyata et al.'s (2011) definition of planning, with the obstacles constituting the 'multiple steps' that must be considered prior to implementing actions. We also attempted to address methodological and procedural issues found to influence performance on previous trap-tube tasks, including the requirement to use tools (Seed et al. 2006; Tebbich et al. 2007), tools being prepositioned in the apparatus (Girndt et al. 2008), having to push the reward away from oneself (Mulcahy and Call 2006b) and a predisposition to avoid displacing rewards over traps (Seed et al. 2006; Seed et al. 2009; Tebbich et al. 2007; Martin-Ordas and Call 2009). These studies showed that subjects' performance may be strongly influenced by procedural features of the experimental design. Therefore, our task uniquely combined the following features:

- (1) It did not require tool-use
- (2) It did not require the reward to be pushed away from the subjects
- (3) It did not always require trap avoidance for the correct response
- (4) It was presented as trial-unique configurations, so that the configuration of obstacles had to be evaluated anew on each trial
- (5) The number of trials was deliberately limited to minimise the possibility of the task being solved using associative learning

In the present study we investigated whether Bornean orangutans were able to solve a task that required them to consider the impact of multiple obstacles on the path of a reward prior to implementing actions to retrieve it. As well as establishing if subjects were able to solve the task, we also examined how they might have been doing this, with regards to what cognitive strategies they might use, allowing us to begin to speculate upon the psychological mechanisms underpinning their decision-making. We predicted that orangutans should perform well in such a task, given that they successfully navigate gaps in the canopy without reaching arboreal 'dead-ends', suggesting that they decide on and follow routes prior to

beginning their travel (Thorpe, personal observation). Furthermore, successful travel requires them to make correct decisions regarding which trees to use and avoid, as an inappropriate choice resulting in a fall, even between canopy levels, may result in serious injury or even death, particularly for larger individuals (Thorpe et al. 2009). As the most distantly related of our great ape relatives, their study is also interesting from a phylogenetic perspective with regards to tracing the emergence of the cognitive capacities related to mental simulation.

Materials and methods

Subjects and housing

Three subjects, all mother-reared and housed at Apenheul Primate Park (Netherlands) participated in the task reported here (see Table 1).

Table 1 Study subjects: sex, age in years and whether they were born in captivity (C) or in the wild (W)

** Table 1 about here **

Eight adult orangutans (six females and two males) were initially identified for participation in the study; however five subjects were dropped following the initial phases (see ‘familiarisation phase’ section below for details). Both indoor and outdoor enclosures were equipped with climbing elements including tree trunks, fibreglass poles, ropes and netting, and enrichment objects such as puzzle feeders were available.

Apparatus

The apparatus was attached to the outside of the enclosure and consisted of an opaque Perspex puzzle-tube (75cm x 12cm x 10cm) with the following components that could be manipulated by the experimenter (see Fig. 1):

- 1) Gap-size of traps: large (4.5cm); medium (3cm); small (2cm)
- 2) Trap direction: forwards (opening towards subject); backwards (opening towards experimenter)

3) Ends configuration: each end could be open or closed

** Fig. 1 about here **

Fig. 1 Apparatus used in the experiment (a) showing interchangeable components: traps with large (1) medium (2) and small (3) gaps that could face either forwards (towards subject) or backwards (towards experimenter), and end pieces (4). The gap sizes were always configured in the order shown in the plan view (b), though the entire configuration could be rotated 180°. The reward (R) is shown in its central starting position for each trial

The apparatus permitted a total of four gaps in the base of the tube (two at each side of the reward's central starting position). The size of the reward (a walnut) meant that it fell through large gaps but could be displaced over small and medium gaps. If the trap beneath a large gap was facing forwards then the reward could be retrieved by the subject (for an example, see Fig. 2c and the online resource ESM_1.mpg; video captions can be found in the online resource ESM_5.pdf). If on the other hand the trap was facing backwards then it was lost by the subject (as shown in Fig. 2d and 2e, and the online resource ESM_2.mpg) and collected by the experimenter and disposed of. The direction that the traps beneath small and medium gaps faced was irrelevant, as the reward never fell into them. At one side of the puzzle-tube there was a small gap followed by a medium gap and at the other side a medium gap followed by a large gap (see Fig. 1b and Fig. 2). The basis for this configuration of gaps was that if subjects only considered the obstacles closest to the reward, i.e. the first gap that must be navigated, then we would expect them to move the reward towards the smaller of the two gaps. Thus, the initial small gap on one side of the tube acted as a perceptual 'lure', because compared to the initial medium-sized gap on the other side it should have seemed that the reward was less likely to fall through, whereas actually it was always followed by a large gap that the reward would fall through. However, as a large gap resulted in the reward being retrieved in some trials but lost in others, trap direction and the configuration of the end pieces also had to be considered. If an end of the tube was open and the two gaps at the same side were small enough for the reward to pass over, then the reward could be retrieved from the end (see Fig.

2a and the online resource ESM_3.mpg). Therefore, because there were multiple obstacles in each direction, subjects needed to look ahead and consider the effect of each obstacle on the reward in order. Only by evaluating all obstacles at both sides of the puzzle-tube (the configuration of gaps, the direction in which the trap beneath the large gap was facing, and whether the end was open or closed) before selecting the initial direction in which to move the reward could subjects achieve perfect performance. However, by attending to some cues but not others performance could still differ from what would be expected by chance (i.e. a 50% success rate; see Results section for detailed explanation).

General procedure

Subjects were tested in separation rooms (10-15m²) where they were held on a regular basis for feeding and cleaning purposes. During the testing phase they were tested in isolation except for one adult female (Sandy) who was accompanied by two dependent juveniles. Subjects were not food deprived before the trials, water was available ad libitum and they could choose to stop participating at any time. The reward in each trial was a walnut and subjects remained motivated to obtain them throughout the study. Subjects manipulated the reward through a series of finger holes (see Fig. 1a) and could retrieve the reward via either an open end of the tube or a forward-facing trap.

Familiarisation phase

All eight potential subjects were presented with the puzzle-tube in its simplest configuration, with a continuous solid base (no gaps or traps) and both ends open. This tested whether the ability to access the reward by rolling it out of either end of the tube was within their sensorimotor repertoire and also familiarised them with the apparatus to minimise the risk of neophobic responses during the testing phase. Four subjects were dropped from the study at this stage due to a lack of interest, motor problems or becoming too nervous or frustrated in the separation areas. Following baseline testing the remaining four subjects then participated in a simpler task (the gap-size task) than the one reported here, consisting of 32

trial-unique configurations that incorporated only a single gap at each side of the tube, which could be small or large (basic methods and data for this task are provided in the online resource ESM_6.pdf). Subsequently a further subject was dropped from the study as she repeatedly attempted to squeeze the reward through the central finger hole rather than moving it in either direction from its central starting position. The remaining subjects that participated in the testing phase were Amos, Sandy and Silvia (see Table 1).

Testing phase

Based on the three puzzle-tube variables (gap-size, trap direction and ends configuration) we generated 64 trial-unique configurations (32 oriented left and right), three schematic examples of which are shown in Fig. 2.

** Fig. 2 about here **

Fig. 2 Three schematic example configurations of the puzzle-tube apparatus showing both gap-size (L= large; M= medium; S= small) and trap-direction (open box= forwards-facing; crossed box= backwards-facing), as well as ends configuration (open or closed). Examples of the correct direction in which to move the reward (direction of arrow) and the access point for obtaining it (head of arrow) are shown (a - c); and the outcome for the same three example configurations if the incorrect direction is chosen (d - f)

Limiting the total number of trials minimised the opportunity for learning across the task and reduced the chance of the task being solved through associative learning and reinforcement. These 64 trials were pseudorandomised into 6 blocks of either 11 (blocks 1-4) or 10 (blocks 5 and 6) trials. Order of block presentation was randomised for each subject. Subjects received one block per day, with session referring to the sequential order in which the blocks were presented.

In each trial, the test subject was presented with the empty apparatus for a preview period of up to 20 seconds, though this was cut short if the subject lost interest in the apparatus or became frustrated. The

reward was then placed in the centre of the puzzle-tube for the subject to manipulate. In each trial the reward could be retrieved if it was moved towards one side but not the other (the ‘correct’ side varied between trials). Fig. 2 shows some schematic examples of the outcomes of moving the reward in the ‘correct’ (Fig. 2a-c) and ‘incorrect’ (Fig. 2d-f) directions.

Data scoring and analysis

All trials were videotaped. For each trial we scored whether the initial choice of direction (defined as the direction in which the subject first moved the reward, even if this was subsequently switched) was correct or incorrect (success), and whether it was to the left or right. Subjects were allowed to correct their mistakes if they chose the incorrect initial direction, so in some ‘incorrect’ trials they eventually went on to retrieve the reward. If a mistake was corrected prior to the reward reaching an impeding obstacle (closed end or large backwards-facing gap) this was scored as ‘self-corrected’. The dependent measure was the percentage of correct responses defined as choosing the correct initial direction in a trial. Two-tailed binomial tests were used to assess whether subjects’ choice of initial direction differed from what would be expected by chance and also whether they showed any directional preferences. The alpha value for the significance level was always 0.05. Data were analysed using PASW Statistics 18 (IBM SPSS Inc. 2009) and R 2.11.1 (LME4 package, R Development Core Team 2010).

Rule simulations

In order to achieve perfect performance, subjects would need to have taken into account all of the obstacles and their spatial relationships. However, they may have achieved partial performance by attending only to certain perceptual cues. We therefore generate simulated outcomes (% correct responses) semi-manually using a computer for the 64 trials based on seven different procedural rules or rule-combinations (see Fig. 4 caption for details of rules) and plotted these together with subjects’ performances. For example, if subjects chose the initial direction based on the procedural rule ‘always move the reward away from the large gap’, we could produce a simulated ‘% correct responses’ outcome

by examining each of the 64 trials in turn and generating an initial choice of direction based on that rule, and whether this would have been correct or incorrect for that particular trial. When a rule did not generate an unambiguous outcome (e.g. ‘always move the reward towards the open end of the tube’ for trials where both ends were open or closed), a direction was chosen at random (random numbers generated in Excel), giving a rule-combination. For such rule-combinations where some trials required the direction to be chosen at random, the simulation was repeated 10 times to give a range of possible outcomes.

GLMMs

To test quantitatively which if any of the puzzle-tube variables had an impact on subjects’ success (correct or incorrect) or initial direction chosen (left or right), we fitted two generalized linear mixed models (GLMMs). Puzzle-tube variables (gap-size, trap direction, ends configuration) were included as fixed factors and subject and session as random factors. We started by fitting the maximal models (including all fixed and random factors) and subsequently removed all non-significant terms to obtain final models.

Results

Amos’ and Sandy’s performances differed significantly from chance-level (50% correct) across the 64 trials (binomial test: 51 out of 64 trials correct; $p < 0.0001$ and 43 out of 64 trials correct; $p = 0.008$ respectively, see Fig.4). Silvia responded correctly in 25 out of 64 trials, which was below chance level but not significantly so (binomial test: $p = 0.103$). Table 1 and Fig. 3 give a summary of subjects’ performance across testing sessions.

Table 2 Summary of performance across sessions

** Table 2 about here **

** Fig. 3 about here **

Fig. 3 Percentage of correct responses by each subject across the six consecutive testing sessions. There was no significant improvement in performance, though Sandy's performance did show a net improvement. Horizontal dotted line indicates chance-level performance (50% correct)

Amos' performance differed significantly from chance level in his first testing session (binomial test: 10 out of 11 trials correct; $p=0.012$; see Table 2). Amos and Sandy both chose the correct initial direction in the first trial in five out of the six testing sessions, including the first trial of their first sessions (Table 2). Amos' performance ranged from 70-91% of trials correct within a session, and Sandy's from 50-91%. Sandy's performance shows a net overall improvement in performance across sessions (Table 2 and Fig. 3); this is tested quantitatively in the GLMMs below. Silvia's best performance was 50% of trials correct in session 4, with her poorest performance occurring in session 2 (30% correct, see Table 2).

Neither Amos nor Sandy showed a directional preference across the 64 trials (binomial test: $p=0.53$ and $p=0.10$, respectively). Silvia on the other hand showed a significant overall preference to move the reward to the right (64.1% of trials; binomial test: $p=0.03$).

Amos did not self-correct in any trials. Sandy self-corrected her initial choice of direction in 2 out of 21 (9.5%) and Silvia in 8 out of 39 (20.5%) incorrect trials. All self-corrections occurred when the impeding obstacle was a closed end of the puzzle-tube; never when it was a large backwards-facing gap. Subjects usually self-corrected following tactile exploration of the closed end.

Rule simulations

Subjects' individual performances and the simulated outcomes based on various rules and rule-combinations are shown in Fig.4. In order to score 100% in this task, subjects would have had to examine all of the obstacles at each side of the tube as no individual cue (e.g. left end open) uniquely identified the side of the tube from which the reward could be retrieved, and hence the correct direction in which to

move the reward. However, it would not be accurate to say that unless subjects did this we would have expected them to perform at chance-level (50% correct). The only scenarios under which we would expect this performance outcome would be if subjects were (a) choosing initial direction at random; (b) had a directional bias to the left or right; or (c) were using the location of the large gap as a cue (see Fig.4).

** Fig.4 about here **

Fig.4 Percentage of correct responses for the three subjects (n=64) and simulated outcomes based on seven procedural rules or rule-combinations: Random = random choice of direction; O end = move reward towards open end of tube; C end = move reward towards closed end of tube (ten simulations; n=640 for each); L gap = move reward towards the large gap; no L gap = move reward away from the large gap (n=64 for each). For simulations in which a rule did not apply to every trial (O end, C end) direction was chosen at random and the simulation repeated ten times (n=640). For boxplots the line across the box is the median and the whiskers indicate the minimum and maximum outcomes for ten repeated simulations. Dotted line indicates chance-level performance (50% correct); dashed box shows that Amos' and Sandy's performances fell within the range of simulated outcomes for the 'O end' rule-combination

Amos' and Sandy's performances both differed significantly from chance-level, suggesting that they were not simply choosing direction at random or based on a directional bias; nor were they only paying attention to the position of the large gap (see Fig.4). However, simulating directional choices for the 64 trials using the rule-combination 'move reward towards open end of the tube; if not applicable choose direction at random' generates a range of outcomes significantly different to 50% correct (64.1 - 81.3%, Fig.4). Both Amos' (79.7% correct) and Sandy's (67.2% correct) performance fell within this range (see dashed box in Fig.4). Silvia's performance did not correspond to any of the simulated outcomes (see Fig.4).

GLMMs

The maximal model (all fixed and random factors included) examining success (correct or incorrect) revealed that only ends-configuration had an impact on subjects' performance across the 64 trials. A model with ends-configuration as the only fixed factor and subject as the only random factor (all other fixed variables and session eliminated) did not differ significantly from the maximal model ($\chi^2=7.38$, d.f.=7, $p=0.39$) so the simpler model was accepted as it had a lower Akaike's Information Criterion (AIC) value (237.3 vs 243.9) (Crawley 2007, pp.353). A second maximal model focussing on the subset of trials in which the ends of the tube were configured one open and one closed ($n=32$) revealed that which end was open was the only fixed factor that had a significant impact on the choice of initial direction. This model did not differ significantly from the simplified model with the fixed factors of gap-size and trap-direction eliminated ($\chi^2=13.25$, d.f.=7, $p=0.07$) so the simpler model was accepted as it had a lower AIC value (116.8 vs 117.6).

In the subset of trials in which the puzzle-tube ends were configured one open and one closed ($n=32$), Amos and Sandy chose the correct initial direction in 90.6% and 87.5% of trials respectively. In the other trials where the ends of the tube were configured the same Amos' performance was the same whether the ends were either both open or both closed (68.8%; $n=32$; $p=0.052$). Sandy's performance in this subset of trials was close to chance-level (46.9%, $n=32$; $p=0.860$), though she performed better when the ends were both closed (56.3% correct; $n=16$) than when they were both open (31.3% correct; $n=16$). Silvia's performance was below chance-level in all subsets of trials.

Discussion

We devised a novel puzzle-tube task that aimed to investigate orangutans' ability to consider the impact of multiple obstacles on the path of a reward prior to implementing actions to retrieve it. When designing the task we aimed to minimise the methodological and procedural concerns of previous studies based on the trap-tube paradigm. We also developed a novel analytical method of rule-simulation for exploring

how subjects may have been attempting to solve the task with regards to what potential procedural rules might have been used.

Two of the three subjects (Amos and Sandy) solved the task (that is, performed significantly above chance) across the 64 trial-unique configurations. More importantly, Amos performed significantly above chance level in his first session, and both successful subjects responded correctly in their initial trial in 5 out of 6 sessions (see Table 2). These results are impressive, given that in previous studies only 2 out of 5 and 2 out of 6 orangutans solved arguably simpler tasks in which they had to learn to avoid a single trap, and required a greater number of trials to do so (Martin-Ordas et al. 2008; Mulcahy and Call 2006b). Furthermore, in both of those studies the only variation between trials was the side on which the trap appeared. Therefore, subjects could have solved the tasks based on the single procedural rule ‘move the reward away from the trap’. In a study by Seed et al. (2009) using a two-trap box that did not require tool-use, all eight chimpanzee subjects learnt to avoid a trap in 40-100 trials. However, only one subject was able to successfully transfer between two tasks that required opposite responses based on the configuration of an arbitrary cue; the other seven continued to use a single procedural rule (‘push toward the shelf piece’) that applied to the previous task (Seed et al. 2009).

Fragaszy et al. (2009) suggested that implementing a forced delay may support the selection of behaviours other than the prepotent one, and there is some evidence to suggest that orangutans may outperform other great ape species in tasks requiring inhibitory control (Vlamings, Hare, and Call 2010). Furthermore, keas were quicker to correct mistakes when opening boxes with multiple locks following a short (10-30 s) preview period (Miyata et al. 2011). It is therefore possible that the preview period in our experiment permitted subjects to look ahead at the multiple obstacles in the puzzle-tube and encouraged mental simulation, though there were no obvious behavioural differences between subjects during this time (Tecwyn, personal observation). Dunbar et al. (2005) did not identify an effect of prior view on chimpanzees’ or orangutans’ speed of retrieving a reward from a puzzle-box. However, in the past

orangutans have frequently been dismissed as “sluggish, slothful and uninteresting” (Russon 2010), which suggests that latency may not have been an appropriate measure of performance due to inter-species behavioural differences. To our knowledge this is also the first time that orangutans have been tested on a trap-tube-like task that does not require tool-use, so it is possible that the additional cognitive load of having to use a tool may have been masking the species’ actual understanding of such tasks in previous experiments, as was found to be the case for chimpanzees (Seed et al. 2009).

What possible strategies could an animal potentially use when attempting to solve a novel problem and how do these relate to our task? *Associative learning and reinforcement* is the mental pairing of events that occur in close temporal and spatial proximity (Taylor et al. 2009). In our task, deliberately limiting the total number of trials reduced the potential for associative learning across trials, and the fact the GLMMs did not reveal a significant effect of testing session on performance (i.e. subjects did not improve significantly at the task with additional trials, see also Fig. 3) suggests that associative learning does not explain the performance of the successful subjects. Amos in particular provides a strong case against learning across trials, as he performed significantly above chance-level in his first testing session. Although it is possible that subjects could have learned relevant associations prior to the study, to our knowledge they had not been presented with any similar apparatus. A puzzle-feeder that had been used by Sandy and Silvia in the past involved using a stick to navigate a reward through a vertical maze, causing it to drop through a series holes and out of the bottom. Amos had never used the puzzle-feeder.

A lack of evidence for learning does not, however, eliminate the possibility that subjects were using a *procedural rule* from the initial trial (Fedor et al. 2008). Such a rule could be based on an arbitrary or relevant cue, and could be appropriate or inappropriate. In contrast to previous similar studies, in our task every trial configuration was unique, and no single cue (e.g. a small gap) individually identified the correct directional response, making it impossible to perform perfectly by using a single procedural rule in relation to a single cue. However, our rule-simulations demonstrated that on our task at least it was

possible to perform well (though not perfectly) by using the 2-rule-combination ‘move reward towards open end of the tube; if not applicable choose direction at random’ (see dashed box in Fig.4). It is feasible that Amos and Sandy were using this rule-combination as both of their performances fell within the range of simulated outcomes for the 64 trials based on it (see Fig.4). The results of the GLMM analyses quantitatively supported the notion that both successful subjects were able to use ends-configuration as a relevant cue for choosing the direction in which to move the reward when one was open and one closed, as they performed better in this subset of trials compared to when both ends of the tube were the same (both open or both closed), and moved the reward towards the open end significantly more than predicted. Furthermore, self-corrections only occurred when the impeding obstacle was a closed end (not a large backwards-facing gap), which suggests that subjects were able to use this as a cue, even if they did not do so prior to choosing their initial direction. Self-correcting may be indicative of a ‘planful’ or forward search strategy, whereby subjects only look ahead to the obstacles in the path of the reward once it has already been moved either left or right (Fragaszy et al. 2003; Pan et al. 2011).

A further possibly more cognitively demanding strategy would be to *mentally simulate* different potential actions and their outcomes for each trial, prior to choosing which direction to move the reward in. Amos performed above chance-level, though not significantly so (68.8% correct; $n=32$; $p=0.052$) in the subset of trials where one open end could not be used as a cue for choosing direction (as both ends were configured the same), which suggests that he may also have been able to use relevant information regarding gap-size and trap-direction to some extent. This suggests that he may have been considering obstacles other than the ends of the tube. Furthermore he was equally able to avoid the large gap and use it to access the reward, as he performed equally well in trials requiring either one of these outcomes. It therefore seems likely that Amos was either using mental simulation to some extent, or was able to use a number of procedural rules flexibly, depending on the configuration of cues in a given trial. Alternatively, subjects could have used mental simulation when initially faced with the task, for example in the first or first few trials, and subsequently construct and use rules based on this limited experience. Fig. 5 shows

that, in fact, subjects could have achieved perfect performance by using three procedural rules based on the three possible configurations of the ends of the tube (also see Fig. 2 for schematic examples of these).

** Fig. 5 about here **

Fig. 5 Subjects could have chosen the correct initial direction in 100% of trials using the three procedural rules shown here, which are based on the configuration of the puzzle-tube ends in a given trial. When the ends of the tube were configured both open or both closed, subjects also needed to consider the position of the large gap

In Fig. 2, subjects could have chosen the correct initial direction in each of the three example configurations shown by using one of the three procedural rules: (a) by following the left-hand rule in Fig. 5; (b) by following the middle rule; and (c) by following the right-hand rule. The left-hand rule would only require the subject to consider the cue ‘ends configuration’, therefore these trials could be solved by following the simple procedural rule ‘move reward towards open end of the tube’ (as in Fig. 2a). The other two rules would require both ‘ends-configuration’ and ‘gap-size’ to be considered (as in Fig. 2b and 2c). The correct initial direction could also have been chosen in the remaining 61 configurations by examining the ends configuration of the puzzle-tube and subsequently using the appropriate procedural rule in Fig. 5. But why would subjects use procedural rules (if indeed this is what they were doing) rather than mentally simulating each trial, and is one approach more cognitively demanding than the other? Shah and Oppenheimer (2008) suggest that the use of heuristic rules in problem-solving, for example examining fewer cues, may reduce cognitive effort (in humans at least) by decreasing the amount of information to be held in working memory at a given time. In our task, subjects could have opted to focus on the cue they deemed to be most important (seemingly the puzzle-tube ends), and where there was a tie on this cue (if both ends were configured the same) they may have examined what they deemed to be the second most important cue (e.g. gap-size, see Fig. 5). Although this may seem contradictory as it still requires multiple cues to be examined, it nonetheless reduces the cognitive demands of the decision-maker as they are only ever considering a single cue at a time (Shah and

Oppenheimer 2008). Mitchell et al. (2009) discuss the use of simulation- versus rule-based approaches in the development of passing false-belief tests in children, and suggest that in this context at least, simulation is the effortful default, with cognitively economical rules being derived from experience over time.

There was substantial between-subject variation in performance on this task, which makes it difficult to generalise about the cognitive mechanisms involved. Even if two individuals' performance was the same it is possible that one could have used heuristic rules to solve the task whereas the other used more abstract reasoning (Chittka and Jensen 2011). However, differences in performance can prove revealing with regards to different strategies used. In a recent study investigating understanding of gravity and solidity in great apes Cacchione and Call (2010) found that different individuals used different strategies when searching for a reward, and not all individuals were able to change strategy flexibly. The use of different strategies may help to explain the differences in performance observed here, with Amos being the most flexible. Sandy may have acquired a correct rule over time, as her performance showed a general but non-significant trend of improvement across sessions (see Table 2). Silvia may have been using an incorrect rule (such as always moving the reward towards the closed end of the tube) which would have led to a systematic error within the subset of trials with the ends configured one open one closed. She did, however, self-correct in more trials than the other two subjects (20.5% of her incorrect trials), which may be indicative of a more 'planful' than 'planned' strategy, as was found to be the case for capuchin monkeys navigating 2D mazes (Pan et al. 2011). As a wild-caught orangutan, it is likely that Silvia's opportunities to gain learning experience in her early years were rather different to the other two subjects (born in captivity), which may have affected her problem-solving behaviour (Lethmate 1979). During a nine year study Galdikas (1982) found that ex-captive orangutans released into the wild exhibited tool-using behaviour in a much wider variety of contexts, compared with wild orangutans. Galdikas attributes this to differential learning experiences during critical learning periods before maturity (Galdikas 1982). Another point worthy of note regarding Silvia is that she was the most difficult subject to encourage to

come to the apparatus (Tecwyn, personal observation), which may be indicative of her lower levels of motivation and attentiveness compared to the other subjects. It is interesting to note that the 9 year old subject performed best, as the four orangutans that solved trap-tube analogous tasks in other studies were all aged between 11-18 years, from a tested range of 6-33 years (Martin-Ordas et al. 2008; Mulcahy and Call 2006b). This study increases the upper age tested to 45 years. It is possible that success in tasks of this nature may be related to age class, as younger orangutans are generally more exploratory of their habitat and its affordances, which is reflected in their larger locomotor repertoire (Thorpe and Crompton 2005, 2006), but a far larger dataset would be required to substantiate this.

In summary, our novel task improved on the methodological and procedural limitations of previous similar tasks and minimised the potential for associative learning across trials by presenting a deliberately limited number of trial-unique configurations. The design of our task did not permit unequivocal conclusions regarding the use of mental simulation to be drawn; rather our use of rule-simulations in the analyses demonstrated that successful subjects could have solved the task by using the 2-rule-combination ‘move reward towards open end of the tube; if not applicable choose direction at random’. GLMMs quantitatively supported the notion that the configuration of the tube ends was used as a cue for choosing direction. This is nevertheless impressive, as performance did not improve significantly across sessions and Amos performed above chance-level in his initial session, suggesting that if these subjects were using a rule-based approach they must have already possessed some appropriate previously acquired causal knowledge (for example the size of a reward relative to a gap and its inability to pass through barriers). Furthermore, the use of rules may in fact be a cognitively economical strategy compared with the mental simulation of each trial (Shah and Oppenheimer 2008). Silvia may have been using an incorrect rule (e.g. move the reward towards the closed end), resulting in a systematic error that contributed to her poor performance, though previous experience, motivation and attention may have also played a key role.

Future studies should develop new paradigms to investigate the cognitive strategies that subjects use when solving tasks that require consideration of multiple steps prior to implementing actions. Ideally, tasks should be constructed in such a way that success via the use of procedural rules is not possible. If the number of steps to be considered between initiation of actions and achieving the desired outcome could be systematically increased (which might be expected to increase cognitive demand (Wimpenny et al. 2009)), a ‘simulation threshold’ could theoretically be reached. It would be particularly interesting to compare the performance of a number of primate species on such tasks to generate a phylogenetic reconstruction of this cognitive ability and to begin to understand the socio-ecological challenges that may have driven its evolution. It is also imperative that future studies continue to look at *how* a task is solved with regards to the underlying cognitive mechanisms, with increased emphasis on detailed analyses of behaviour, as it seems that such studies with primates are now falling behind those conducted with birds (see e.g. Miyata et al. 2011; Wimpenny et al. 2009).

Acknowledgements We thank Apenheul Primate Park (Netherlands) for granting permission for scientific research and generously giving their time, support and valuable knowledge. Special thanks go to Rudy Berends, Leo Hulsker, Bianca Klein and Frank Rietkerk. We are also grateful to four anonymous reviewers whose comments contributed to the improvement of this manuscript. This study was funded by a Natural Environment Research Council studentship to E.C.T.

Ethical standards The experiments reported here comply with the current laws of the country (Netherlands) in which they were performed.

Conflict of interest The authors declare that they have no conflict of interest

References

- Bard KA (1995) Sensorimotor Cognition in Young Feral Orangutans (*Pongo-Pygmaeus*). *Primates* 36:297-321
- Biro D, Matsuzawa T (1999) Numerical ordering in a chimpanzee (*Pan troglodytes*): Planning, executing, and monitoring. *J Comp Psychol* 113:178-185
- Brewer SM, McGrew WC (1990) Chimpanzee use of a tool-set to get honey. *Folia Primatol* 54:100–104
- Byrne RW (1997) The Technical Intelligence hypothesis: An additional evolutionary stimulus to intelligence? In: Whiten A and Byrne RW (eds), *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge University Press, Cambridge, pp 289-311
- Byrne RW, Corp N, Byrne JME (2001) Estimating the complexity of animal behaviour: how mountain gorillas eat thistles. *Behaviour* 138:525–557
- Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn Sci* 12:187-192
- Carruthers P (1998) Natural theories of consciousness. *Eur J Philos* 6:203-222
- Chevalier-Skolnikoff S, Galdikas BMF, Skolnikoff AZ (1982) The adaptive significance of higher intelligence in wild orang-utans: a preliminary report. *J Hum Evol* 11:639-652
- Chittka L, Jensen K (2011) Animal Cognition: Concepts from Apes to Bees. *Curr Biol* 21:116-119
- Corp N, Byrne RW (2002) Leaf processing by wild chimpanzees: physically defended leaves reveal complex manual skills. *Ethology* 108:673–696
- Crawley MJ (2007) *The R book*. John Wiley & Sons Ltd, Chichester
- Dunbar RIM, McAdam MR, O'Connell S (2005) Mental rehearsal in great apes (*Pan troglodytes* and *Pongo pygmaeus*) and children. *Behav Proc* 69:323-330
- Dufour V, Sterck EHM (2008) Chimpanzees fail to plan in an exchange task but succeed in a tool-using procedure. *Behav Proc* 79:19-27
- Epstein R, Kirshnit CE, Lanza RP, Rubin LC (1984) 'Insight' in the pigeon: antecedents and determinants of an intelligent performance. *Nature* 308:61-62
- Fedor A, Skollar G, Szerencsy N, Ujhelyi M (2008) Object Permanence Tests on Gibbons (*Hylobatidae*). *J Comp Psychol* 122:403-417

- Fragaszy D, Johnson-Pynn J, Hirsh E, Brakke K (2003) Strategic navigation of two-dimensional alley mazes: comparing capuchin monkeys and chimpanzees. *Anim Cogn* 6:149-160
- Fragaszy DM, Kennedy E, Murnane A, Menzel D, Brewer G, Johnson-Pynn J, Hopkins W (2009) Navigating two-dimensional mazes: chimpanzees (*Pan troglodytes*) and capuchins (*Cebus apella* sp.) profit from experience differently. *Anim Cogn* 12:491-504
- Frith CD, Frith U (1999) Interacting Minds-A Biological Basis. *Science* 286:1692-1695
- Galdikas BMF (1982) Orang-utan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo (Kalimantan Tengah). *J Hum Evol* 11:19-33
- Girndt A, Meier T, Call J (2008) Task constraints mask great apes' ability to solve the trap-table task. *J Exp Psychol Anim B* 34:54-62
- Hihara S (2003) Rapid learning of sequential tool use by macaque monkeys. *Physiol Behav* 78:427-434
- Kacelnik A (2009) Tools for thought or thought for tools? *PNAS* 106:10071-10072
- Kuczaj SA, Gory JD, Xitco MJ (2009) How intelligent are dolphins? A partial answer based on their ability to plan their behavior when confronted with novel problems. *Jpn J Anim Psychol* 59:99-115
- Lethmate J (1979) Instrumental Behaviour of Zoo Orang-utans. *J Hum Evol* 8:741-744
- Lethmate J (1982) Tool-using skills of orang-utans. *J Hum Evol* 11:49-64
- Martin-Ordas G, Call J (2009) Assessing generalization within and between trap tasks in the great apes. *Int J Comp Psychol* 22:43-60
- Martin-Ordas G, Call J, Colmenares F (2008) Tubes, tables and traps: great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Anim Cogn* 11:423-430
- Mitchell P, Currie G, Ziegler F (2009) Two routes to perspective: Simulation and rule-use as approaches to mentalizing. *Brit J Dev Psychol* 27:513-543
- Miyata H, Gajdon GK, Huber L, Fujita K (2011) How do keas (*Nestor notabilis*) solve artificial-fruit problems with multiple locks? *Anim Cogn* 14:45-58
- Mulcahy NJ Call J (2006a) Apes save tools for future use. *Science* 312:1038-1040
- Mulcahy NJ, Call J (2006b) How great apes perform on a modified trap-tube task. *Anim Cogn* 9:193-199
- Osvath M (2009) Spontaneous planning for future stone throwing by a male chimpanzee. *Curr Biol* 19:190-191

Osvath M, Osvath H (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Anim Cogn* 11:661-674

Pan J, Kennedy EH, Pickering T, Menzel CR, Stone BW, Fragaszy DM (2011) Development of maze navigation by tufted capuchins (*Cebus apella*). *Behav Proc* 86:206-215

Povinelli DJ, Cant JGH (1995) Arboreal clambering and the evolution of self-conception. *Q Rev Biol* 70:393-421

Premack DG, Woodruff G (1978) Does the chimpanzee have a theory of mind? *Behav Brain Sci* 1:515-526

Raby CR, Alexis DM, Dickinson A, Clayton NS (2007) Planning for the future by western scrub-jays. *Nature* 445:919-921

Raby CR, Clayton NS (2009) Prospective cognition in animals. *Behav Proc* 80:314-324

Russon AE (2010) Life history: the energy-efficient orangutan. *Curr Biol* 20:981-983

Santos LR, Rosati A, Sproul C, Spaulding B, Hauser MD (2005) Means-means-end tool choice in cotton-top tamarins (*Saguinus oedipus*): finding the limits on primates' knowledge of tools. *Anim Cogn* 8:236-246

Shah A, Oppenheimer D (2008) Heuristics made easy: an effort-reduction framework. *Psych Bull* 134:207-222

Seed AM, Call J, Emery NJ, Clayton NS (2009) Chimpanzees solve the trap problem when the confound of tool-use is removed. *J Exp Psychol Anim B* 35:23-34

Seed AM, Tebbich S, Emery NJ, Clayton NS (2006) Investigating physical cognition in rooks, *Corvus frugilegus*. *Curr Biol* 16:697-701

Suddendorf T, Corballis MC, Collier-Baker E (2009) How great is great ape foresight? *Anim Cogn* 12:751-754

Suddendorf T, Whiten A (2001) Mental Evolution and Development: Evidence for Secondary Representation in Children, Great Apes, and Other Animals. *Psych Bull* 127:629-650

Taylor AH, Elliffe D, Hunt GR, Gray RD (2010) Complex cognition and behavioural innovation in New Caledonian crows. *Proc R Soc B* 277:2637-2643

Taylor AH, Hunt GR, Holzhaider JC, Gray RD (2007) Spontaneous metatool use by New Caledonian crows. *Curr Biol* 17:1504-1507

Taylor AH, Hunt GR, Medina FS, Gray RD (2009) Do New Caledonian crows solve physical problems through causal reasoning? *Proc R Soc B* 276:247-254.

Tebbich S, Seed AM, Emery NJ, Clayton NS (2007) Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem. *Anim Cogn* 10:225-231

- Thorpe SKS, Crompton RH (2005) Locomotor ecology of wild orangutans (*Pongo pygmaeus abelii*) in the Gunung leuser ecosystem, Sumatra, Indonesia: A multivariate analysis using log-linear modeling. *Am J Phys Anthropol* 127:58-78
- Thorpe SKS, Crompton RH (2006) Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. *Am J Phys Anthropol* 131:384-401
- Thorpe SKS, Crompton RH, Alexander R McN (2007) Orangutans use compliant branches to lower the energetic cost of locomotion. *Biol Letters* 3:253-256
- Thorpe SKS, Holder R, Crompton RH (2009) Orangutans employ unique strategies to control branch flexibility. *PNAS* 106:12646-12651
- Visalberghi E, Limongelli L (1994) Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *J Comp Psych* 108:15-22.
- Vlamings PHJM, Hare B, Call J (2010) Reaching around barriers: the performance of the great apes and 3-5-year-old children. *Anim Cogn* 13:273-285
- Wimpenny JH, Weir AAS, Clayton L, Rutz C, Kacelnik A (2009) Cognitive processes associated with sequential tool use in New Caledonian crows. *PLoS ONE* 4:e6471

Captions

Table 1 Study subjects: sex, age in years and whether they were born in captivity (C) or in the wild (W)

Table 2 Summary of performance across sessions

Fig. 1 Apparatus used in the experiment (a) showing interchangeable components: traps with large (1) medium (2) and small (3) gaps that could face either forwards (towards subject) or backwards (towards experimenter), and end pieces (4). The gap sizes were always configured in the order shown in the plan view (b), though the entire configuration could be rotated 180°. The reward (R) is shown in its central starting position for each trial

Fig. 2 Three schematic example configurations of the puzzle-tube apparatus showing both gap-size (L= large; M= medium; S= small) and trap-direction (open box= forwards-facing; crossed box= backwards-facing), as well as ends configuration (open or closed). Examples of the correct direction in which to move the reward (direction of arrow) and the access point for obtaining it (head of arrow) are shown (a - c); and the outcome for the same three example configurations if the incorrect direction is chosen (d - f)

Fig. 3 Percentage of correct responses by each subject across the six consecutive testing sessions. There was no significant improvement in performance, though Sandy's performance did show a net improvement. Horizontal dotted line indicates chance-level performance (50% correct)

Fig. 4 Percentage of correct responses for the three subjects (n=64) and simulated outcomes based on seven procedural rules or rule-combinations: Random = random choice of direction; O end = move reward towards open end of tube; C end = move reward towards closed end of tube (ten simulations; n=640 for each); L gap = move reward towards the large gap; no L gap = move reward away from the large gap (n=64 for each). For simulations in which a rule did not apply to every trial (O end, C end) direction was chosen at random and the simulation repeated ten times (n=640). For boxplots the line across the box is the median and the whiskers indicate the minimum and maximum outcomes for ten repeated simulations. Dotted line indicates chance-level performance (50% correct); dashed box shows that Amos' and Sandy's performances fell within the range of simulated outcomes for the 'O end' rule-combination

Fig.5 Subjects could have chosen the correct initial direction in 100% of trials using the three procedural rules shown here, which are based on the configuration of the puzzle-tube ends in a given trial. When the ends of the tube were configured both open or both closed, subjects also needed to consider the position of the large gap

Table 1

Subject	Sex	Age	Birthplace
Amos	M	9	C
Sandy	F	27	C
Silvia	F	44	W

Table 2

Session	Amos			Sandy			Silvia		
	% correct	1 st trial correct?	block	% correct	1 st trial correct?	block	% correct	1 st trial correct?	block
1	91	Y	4	60	Y	5	36	N	4
2	80	Y	6	50	Y	6	30	Y	5
3	73	N	3	64	N	1	36	N	2
4	91	Y	1	64	Y	2	50	Y	6
5	73	Y	2	73	Y	3	36	N	1
6	70	Y	5	91	Y	4	45	Y	3

Fig.1

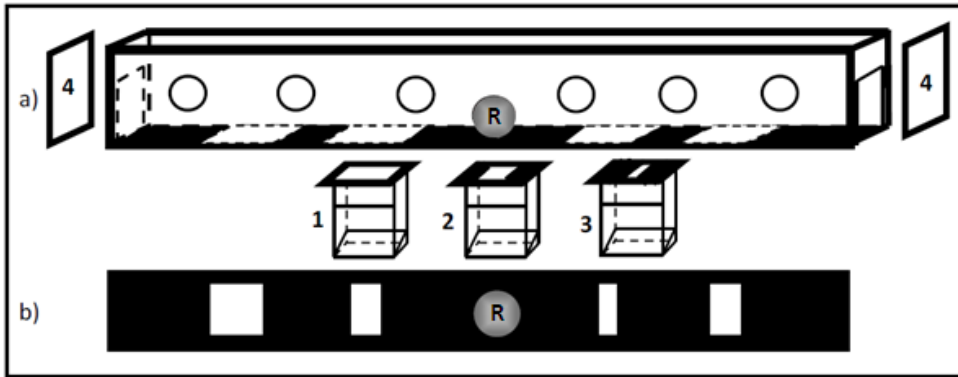


Fig. 2

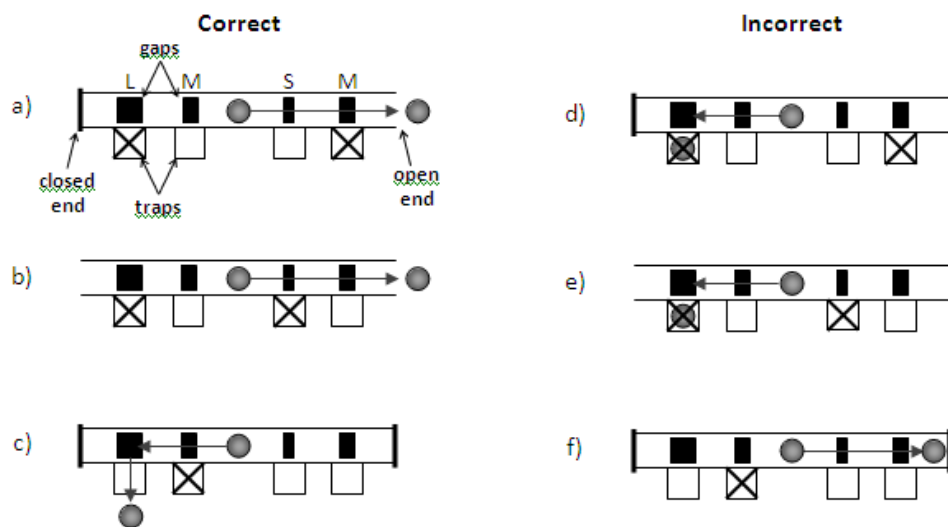


Fig. 3

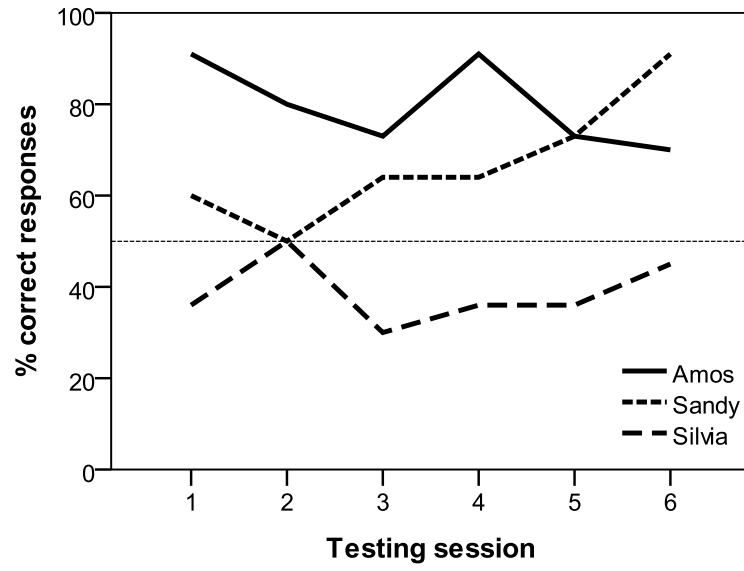


Fig. 4

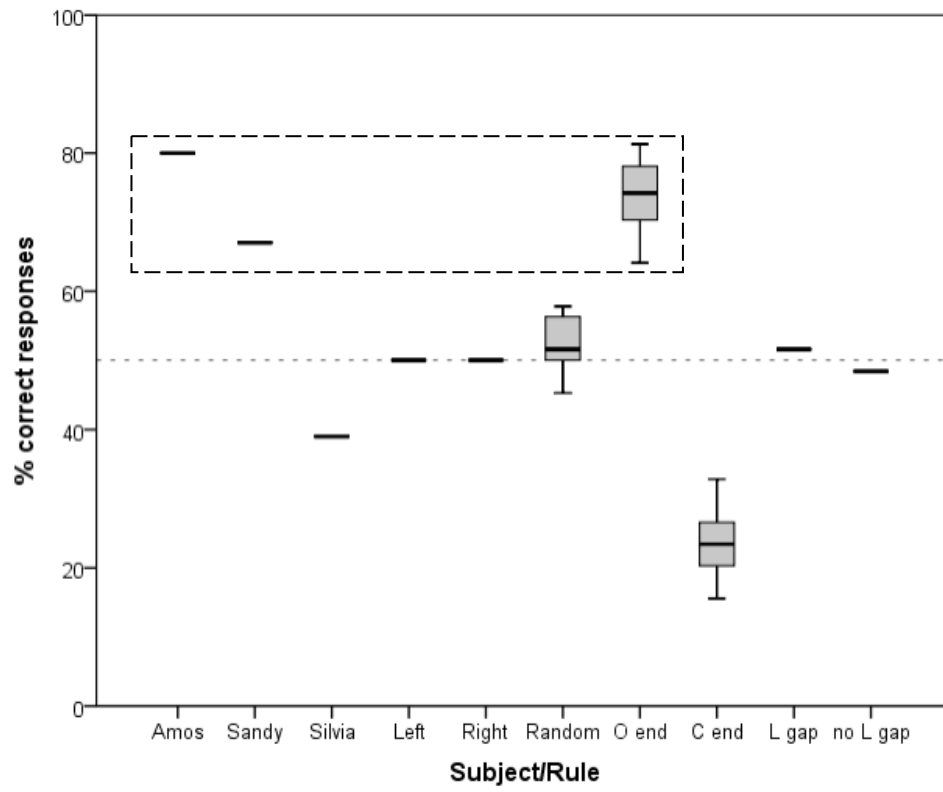


Fig. 5

