A novel test of planning ability: Great apes can plan step-by-step but not in advance of action

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ABSTRACT

The ability to identify an appropriate sequence of actions or to consider alternative possible action sequences might be particularly useful during problem solving in the physical domain. We developed a new 'paddle-box' task to test the ability of different ape species to plan an appropriate sequence of physical actions (rotating paddles) to retrieve a reward from a goal location. The task had an adjustable difficulty level and was not dependent on species-specific behaviours (e.g. complex tool use). We investigated the planning abilities of captive orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) using the paddle-box. In experiment 1, subjects had to rotate one or two paddles before rotating the paddle with the reward on. Subjects of both species performed poorly, though orangutans rotated more non-food paddles, which may be related to their greater exploratory tendencies and bolder temperament compared with bonobos. In experiment 2 subjects could always rotate the paddle with the reward on first and still succeed, and most subjects of both species performed appropriate sequences of up to three paddle rotations to retrieve the reward. Poor performance in experiment 1 may have been related to subjects' difficulty in inhibiting the prepotent response to act on the reward immediately.

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1. Introduction

Planning as an everyday concept has many connotations, and several terms are used more or less interchangeably to describe a myriad of behaviours that do not seem to have much in common (Parrila et al., 1996). At one end of the spectrum, planning can consist of anticipating the consequences of motor actions, for example grasping an object in an appropriate orientation (end-state comfort effect; Rosenbaum et al., 1990). This has been demonstrated to develop early in humans (by 19 months of age; McCarty et al., 1999) and also to have emerged early in primate phylogeny, being present in several lemur species (Chapman et al., 2010). At the other end of the spectrum lies episodic future thinking: the ability to mentally project oneself into an imagined future scenario (Suddendorf and Corballis, 1997). There is continuing debate regarding which, if any, nonhuman species possess this latter capacity, with some researchers presenting experimental evidence for animals imagining and planning for future events (Mulcahy and Call, 2006; Osvath, 2009; Osvath and Karvonen, 2012; Osvath and Osvath, 2008; Raby et al., 2007) and others arguing that foresight is an uniquely human ability (Suddendorf and Corballis, 2007; Suddendorf et al., 2009). Clearly, these two examples of planning, and the multitude of

intermediate cases, must pose very different cognitive demands and vary in terms of their information processing requirements (Chappell et al., 2012; Tecwyn et al., 2012).

Bearing this in mind, it is important to specify the type of planning that is of interest here, which is the type of planning that may be involved in problem solving that is oriented towards current needs. This can be defined as the ability to identify an appropriate sequence of actions or consider alternative courses of action prior to execution (see Tecwyn et al., 2012 for further discussion). Behaviours exhibited by wild great apes that may involve this type of planning include the use of 'tool-sets' for extractive foraging of honey by chimpanzees (*Pan troglodytes*: Brewer and McGrew, 1990); 'engineering' of alliances with the most profitable partners by bonobos (*Pan paniscus*; Aureli et al., 2008; Hohmann and Fruth, 2002); hierarchical processing of plant material by gorillas (*Gorilla beringei beringei*: Byrne et al., 2001) and gap-crossing in the compliant forest canopy by orangutans (*Pongo pygmaeus*: Chevalier-Skolnikoff et al., 1982).

How might planning for current needs be investigated experimentally? Several papers have advocated developing experimental methodologies and paradigms that consider different species' predispositions to allow testing of multiple species (Santos et al., 2006; Amici et al., 2010; MacLean et al., 2012), as at present systematic interspecific comparisons are still rare (Schmitt et al., 2012). This is important in order to avoid the presentation of tasks in an 'unfair' manner, hence biasing for or against the abilities of certain species (Roth and Dicke, 2005). To date, studies investigating planning

for current needs in nonhuman species have mostly fallen in to one of two categories: those involving the use of tools, and those involving computerised interfaces (but see e.g. Dunbar et al., 2005; Kuczaj et al., 2009; Miyata et al., 2011 for interesting alternative approaches).

Tool-use studies of planning, usually focused on sequential tool-use, or metatool use (e.g. Bird and Emery, 2009; Hihara, 2003; Martin-Ordas et al., 2012; Mulcahy et al., 2005; Taylor et al., 2007, 2010; Wimpenny et al., 2009) have yielded many interesting insights. However, they may not be ideal when attempting to develop a comparative planning paradigm, for at least two reasons. First, they bias against non-tool-using species, as the behaviours involved in solving the task may not form part of their natural repertoire, and may require fairly precise manipulatory abilities (e.g. sufficient motor control to hold a stick and insert it into a narrow tube). Second, there is evidence to suggest that removing tool-use from physical cognition problems can reduce cognitive load and improve performance (Seed et al., 2009). Therefore, if it is planning rather than tool-use that is the focus of study, it seems prudent to avoid the requirement for tool-use.

Studies involving computerised environments have also been used to investigate planning ability. These require subjects to use either a touch-screen or joystick, for example to navigate through a two-dimensional maze (e.g. Fragaszy et al., 2003, 2009; Miyata and Fujita, 2008; Pan et al., 2011) or to recall a sequence of numbers (Beran et al., 2004; Biro and Matsuzawa, 1999). Such techniques certainly have experimental advantages, such as precise timing of stimulus presentation and automatic recording of behavioural responses. However, they are expensive and time-consuming to implement, with subjects requiring extensive training to use the experimental apparatus prior to the start of testing. Furthermore, the physical and temporal distance between stimulus, response and reward, and the need for refined motor abilities can be problematic, particularly for younger individuals (Mandell and Sackett, 2008).

A further problem with these and other cognitive tasks such as the trap-tube paradigm (Visalberghi and Limongelli, 1994) is that initial errors made by the subject are often correctable. In trap-tube tasks for example, the reward can initially be moved in one direction, but the direction could be switched before the reward falls in a trap. Although error correction strategies can be enlightening (e.g. DeLoache et al., 1985), having the option of correcting an error may reduce the motivation of subjects to make the correct choice in the first place, or to plan for the correct solution (Tecwyn et al., 2012).

As well as considering the practical and paradigmatic issues raised above, it has been suggested recently by MacLean et al. (2012) that it would be fruitful for researchers to design tasks with an adjustable level of difficulty, in order to avoid the masking of meaningful variation due to floor or ceiling effects. In the case of planning during problem solving, it would be useful to have a task that could distinguish between, for example, the ability to make selections between alternatives (proto-deliberative; Sloman, 2010) and the ability to explore branching futures (fully deliberative; Sloman, 2010), which differ in terms of their computational burden.

The aims of this paper were two-fold. First, we aimed to design a new paradigm appropriate for comparative testing of planning ability in primate species (including humans) that:

- Did not involve complex tool-use
- Did not depend on species-specific behaviours/competences
- Had an adjustable level of difficulty
- Did not have a performance outcome that was dependent on a binary choice, in order to reduce the possibility of the task being solved by chance

- Was not correctable, to encourage subjects to choose correctly initially
- Could be configured in a trial-unique manner, so the task had to be considered anew for each trial.

Second, we aimed to use the new paradigm to investigate whether captive bonobos and orangutans (*Pongo pygmaeus*) are able to plan an appropriate sequence of actions (a) in advance (experiment 1); or (b) sequentially (experiment 2), in order to retrieve a food reward from a goal location. These species are of particular interest in the investigation of planning abilities from a comparative perspective because they represent our closest and most distant great ape relatives, respectively, and therefore potentially allow inferences regarding the evolution of planning ability to be drawn (Mulcahy and Call, 2006). If the ability to plan was present in the great ape last common ancestor, then we might expect both bonobos and orangutans to exhibit planning behaviour. If it evolved more recently in an African ape ancestor, then we might expect only bonobos to perform well in our planning task. If on the other hand orangutans outperform bonobos, this may suggest that orangutans have refined their adaptations (both anatomical and cognitive) for arboreal living, beyond those that were present in the great ape common ancestor. As the only great ape species to remain in the terminal branch niche (Grand, 1972) and therefore still face the locomotor demands as posited by Povinelli and Cant (1995), it seems feasible that orangutans have continued to face strong selection pressure for the ability to mentally 'try out' different possible courses of action, and may therefore potentially possess particularly refined planning skills.

2. Methods

2.1. Subjects and housing

Four bonobos housed at Twycross Zoo, UK and eight orangutans housed at Apenheul Primate Park and Ouwehands Dierenpark Rhenen in the Netherlands, participated in this study.

Not all subjects participated in all of the experiments, and in some experiments the number of trials completed varied between subjects. This was to comply with zoo-specific regulations relating to research. Details of which individuals participated in which experiments are given in Table 1 as well as the separate methods sections for each experiment below. The number of trials completed by different individuals is specified in the relevant sections. Bonobos at Twycross and orangutans at Ouwehands were naive with respect to cognitive testing, whereas orangutans at Apenheul had previously been exposed to a trap-tube type task reported in Tecwyn et al. (2012). The bonobos at Twycross Zoo were housed as two separate subgroups in one indoor building ($124\,m^2$) and shared an outdoor enclosure ($588\,m^2$), which the two subgroups had access to at different times during the day. They were fed a range of fruits and vegetables twice daily, and received additional feeds of egg, bread or cheese once or twice per week. Of the subjects that participated in this study, Keke, Banya and Kichele were in one subgroup and Cheka was in the other subgroup. The orangutans at Apenheul Primate Park were housed in four interconnected indoor enclosures (total $232\,m^2$) and had access to eight outdoor islands (total $1000\,m^2$). The orangutans at Ouwehands Dierenpark were housed in three interconnected indoor enclosures (total $370\,m^2$) and had access to an outdoor enclosure ($348\,m^2$). They also had access to an outdoor system of ropes connected to wooden poles at a height of approximately 10 m, which extended out of the enclosure. Orangutans in both facilities were fed a range of fruits and vegetables two to three times per day, as well as ape biscuits/pellets. They received additional feeds of egg or bread two or three times