

Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use

Mathias Osvath · Helena Osvath

Received: 26 September 2007 / Revised: 21 April 2008 / Accepted: 12 May 2008
© Springer-Verlag 2008

Abstract Planning for future needs has traditionally been considered to be restricted to human cognition. Although recent studies on great ape and corvid cognition challenge this belief, the phylogenesis of human planning remains largely unknown. The complex skill for future planning has not yet been satisfactorily established in any other extant primate species than our own. In humans, planning for future needs rely heavily on two overarching capacities, both of which lie at the heart of our cognition: self-control, often defined as the suppression of immediate drives in favor of delayed rewards, and mental time travel, which could be described as a detached mental experience of a past or future event. Future planning is linked to additional high complexity cognition such as metacognition and a consciousness usually not attributed to animals. In a series of four experiments based on tool use, we demonstrate that chimpanzees (*Pan troglodytes*) and orangutans (*Pongo abelii*) override immediate drives in favor of future needs, and they do not merely rely on associative learning or semantic prospection when confronted with a planning task. These results suggest that great apes engage in planning for the future by out competing current drives and mentally pre-experiencing an upcoming event. This suggests that the advanced mental capacities utilized in human future planning are shared by phylogenetically more ancient species than previously believed.

Keywords Planning · Mental time travel · Self-control · Bischof–Köhler-hypothesis · Animal consciousness

Introduction

It is commonly argued that the skill to plan for future needs is exclusive to humans (e.g., Atance and O’Neill 2001, 2005; Gilbert and Wilson 2007; Gulz 1991; Köhler 1921, 1925; Noble and Davidson 1996; Premack 2007; Roberts 2002, 2006; Suddendorf and Busby 2005, Suddendorf and Corballis 1997, 2007; Tulving 2005). The assertion that non-humans are unable to use flexible cognitive prospection beyond the present need is dubbed the Bischof–Köhler hypothesis (Suddendorf and Corballis 1997). Undoubtedly, such future need planning plays a decisive role in human life and society, at the same time it is tremendously difficult to observe the behaviors of non-humans. Observational reports on future planning in animals barely exists, and the few that do (Boesch and Boesch-Acherman 2000; Byrne 1995; de Waal 1982), fail to give unequivocal accounts as they represent single occasions or do not rule out alternative interpretations. Surprisingly, only modest experimental efforts have been made to settle the question whether this pivotal skill is unique to humans. This study explores some central aspects of forethought in great apes, and addresses the Bischof–Köhler hypothesis.

Even though planning always concerns the future, not all future oriented behaviors are the result of planning. The flexible cognition required for planning is not necessary in a range of common anticipatory activities such as nesting, hibernation, migration or food hoarding. In many species, such behaviors appear to rely on comparably rigid and innate mechanisms.

Planning skills could be divided into levels of complexity and might be theoretically approached from different angles. An important distinction is between planning for present needs and planning for future needs (e.g., Byrne 1995; Gulz 1991). Many animals seem to solve sequential

M. Osvath (✉) · H. Osvath
Lunds University Cognitive Science, Lund, Sweden
e-mail: mathias.osvath@lucs.lu.se

problems in order to fulfill present drives, thus making planning for immediate needs a rather spread activity in nature. The skill for immediate need planning is in itself a conglomerate of cognitive sub-mechanisms. Even if different species share the capacity for immediate planning, they might still differ from each other in the complexity of the skill. The topic of this study, however, is the other aspect of planning.

In humans, planning for future needs involves two broad and fundamental cognitive capacities (e.g., Atance and O'Neill 2005; Szpunar et al. 2007), both essential in our cognition. The first is an inhibitory capacity that may be summarized as the exercise of self-control, often defined as the suppression of immediate drives in favor of delayed rewards (e.g., Ainslie 1974; Mischel et al. 1989). The second is a capacity to construct mental experiences of potential events, something that could be expressed as a projection of the self into possible future events, regularly referred to as mental time travel (e.g., Suddendorf and Busby 2005; Suddendorf and Corballis 1997, 2007; Tulving 2005). In humans, both these abilities develop fairly late and around the same age, at about 3–5 years (Atance and O'Neill 2005; Suddendorf and Busby 2005). Self-control and mental time travel are vital concepts in the understanding and testing of the Bischof–Köhler hypothesis, as shall be dealt with in detail further.

Self-control is typically measured by letting subjects choose between smaller immediate rewards and larger delayed rewards (e.g., Tobin and Logue 1994). This is as an operationalization of a broad inhibitory ability involved in an array of cognitive operations. Without self-control, an immediate reward evokes a motivation stronger than the one for obtaining a larger future reward, and as a consequence any plans for future needs cannot govern the behavior at that time. Self-control is studied in a range of paradigms, from animal cognition to economics, and is recognized as a demanding ability profoundly integrated in human cognition. Levels of self-control in humans correlate strongly with a variety of complex cognitive abilities, and predict individual success in domains as diverse as interpersonal skills, psychopathology and academic achievement (Mischel et al. 1989; Tangney et al. 2004; Carlson and Moses 2001; Duckworth and Seligman 2005). The human capacity is often considered unparalleled and allows us to wait for hours, or even years, to obtain a reward (e.g., Fredrick et al. 2002). In contrast, the self-control displayed by animals is characteristically restricted to extremely short delays between the smaller and the larger reward (Ramseyer et al. 2006; Roberts 2002, 2006; Stevens et al. 2005). The impulsivity of animals is one of the main reasons for the assumption that they are mentally stuck in the present time (Köhler 1921; Roberts 2002, 2006). Nevertheless, some studies show that chimpanzees have well-developed

self-control (Beran et al. 1999; Beran and Evans 2006; Evans and Beran 2007; Rosati et al. 2007). One study even suggests that chimpanzees are comparable to humans in self-control tasks involving food rewards (Rosati et al. 2007). This indicates that great apes should be suitable for complex planning skill investigations. It is worth noting that, as a testament to the cognitive tightrope act behind self-controlled behavior, humans regularly fail to override immediate drive states to obtain delayed gratification (e.g., Ainslie 2001).

Mental time travel is thought by many to be exclusive to human thinking (e.g., Gilbert and Wilson 2007; Suddendorf and Busby 2005; Suddendorf and Corballis 1997, 2007; Tulving 2005;). The ability is closely connected to the concept of episodic memories, first described by Tulving (1972). Episodic memories enable us to recall something as opposed to just know something, which is semantic memory. For instance, we know that most boats float on water (semantic memory) but we can actually recall occasions when we personally have taken boat rides or have seen floating boats (episodic memory). This recall constitutes the retrospective part of mental time travel. The forward part, projecting into possible futures, is most likely based on the same cognitive system as episodic memories, and hence involves a form of mental life-like experience as opposed to a mere knowledge about upcoming events. The system constructs and reconstructs events mentally rather than purely constituting a memory structure (e.g., Atance and O'Neill 2001, 2005; Suddendorf and Busby 2005; Suddendorf and Corballis 1997, 2007; Tulving 2005). Accumulated neurological data confirm that prospection and retrospection, and perhaps even theory of mind, rely on the same core brain network (for review see Buckner and Carroll 2007). The defining character of an episodic system in use is the experience of a first person view of re- or pre-experienced events. In humans, envisioning a non-present situation is the key feature of mental time travel (e.g., Gilbert and Wilson 2007; Szpunar et al. 2007). Naturally, other modalities than vision also contribute to this mental re- or pre-experience. Such travels, with their first person perspectives, involve a certain form of self-consciousness allegedly limited to human cognition (Tulving 2005; Gardiner 2002; Macphail 1998).

In this context, it must be noted that a prospective system analogous to the semantic memory system of declarative general knowledge has been suggested (Suddendorf and Corballis 2007). This semantic prospection system allows its owner to voluntarily apply knowledge acquired in one situation onto another. Semantic prospection is rule-based and thereby only sensitive to regularities of potential future events, as opposed to the episodic system that by pre-experience pick out particularities of the possible future events.

Behavioral experiments suggesting episodic-like memories in, for example, corvids and primates (e.g., Clayton and Dickinson 1998, 1999; Schwartz et al. 2005) are partly disputed, mainly because the studies are claimed to be inadequate in ruling out associative learning or species-specific behaviors (Suddendorf and Corballis 2007; Tulving 2005; Roberts 2002, 2006). The question about the related skill of episodic prospection in non-humans will be dealt with further. However, it should be mentioned that the specific brain state at wakeful rest, that is strongly linked to mental self-projection in humans (e.g., Christoff et al. 2004; Andreasen et al. 1995; Ingvar 1979), has currently been reported to have a counterpart in chimpanzees (Rilling et al. 2007).

Behavioral criteria of this study

Behavioral criteria are obviously the *sine qua non* of establishing prospective cognition in non-humans (e.g., Suddendorf and Corballis 2007; Suddendorf and Busby 2005; Tulving 2005). Consequently a detailed discussion must be devoted to the criteria that are specifically set and adhered to in this study. An examination of the meaning of the Bischof–Köhler hypothesis reveals the intertwining of self-control and episodic prospection and their central role in testing the hypothesis. The latest version of the Bischof–Köhler hypothesis states: “[...] only humans can flexibly anticipate their own future mental states of need and act now to secure them” (Suddendorf and Corballis 2008). The expression “flexibly anticipate” relates to cognitive operations that represent the particularities of a future event, which implies episodic pre-experiencing, and hence excludes innate mechanisms, associative learning and apparently even semantic prospection. The phrase “mental states of need” is somewhat more intricate to construe, particularly given the much-debated status of these concepts dating back to, at least, the seminal work of Maslow (1943). However, “need” could in this context simply be viewed, somewhat circularly, as something that is expressed as a motivation to reduce the need, and not necessarily as a life-supporting biological need. This interpretation assumes that “mental states” is equivalent to a drive state. A typical example of such a drive state would be a desire of some sort. The latter part of the hypothesis pinpoints the key act of planning execution, describing the ability to act in the present in order to secure the anticipated need. The motivation for future planning must be stronger than the motivation to act for the present situation; a well-developed inhibitory capacity is required.

The adoption of the self-control paradigm in the investigation of planning skills in non-humans proves fruitful for several reasons. This was appreciated early on in the field

when Wolfgang Köhler pointed out the importance, in the context of chimpanzee forethought, of finding behaviors where an immediate interest is disregarded in favor of a future interest (Köhler 1921). The merits of the self-control paradigm are immediately palpable in relation to the end section of the Bischof–Köhler hypothesis. A specifically designed self-control setting creates a decisive test of the ability to act in the present to ensure the satisfaction of a future need. To decline the immediate satisfaction of one drive in favor of a future oriented one is arguably a most taxing planning situation. The rejection not only requires patience, but also tolerance against the discomfort of not getting the immediate satisfaction.

Less obvious, perhaps, is the methodological strength of the self-control setting when contrasted with what appears to be a prevailing experimental approach of the field. A common example of prospective mental time travel is the ability to foresee a drive that is currently satiated (e.g., Suddendorf and Corballis 2007; Correia et al. 2007). Experiments based on this view ensure that the drive state of the need that is planned for is satiated during the prospective actions. However, anticipation under such circumstances could be served by semantic prospection than by an episodic process. Besides being introspectively intuitive, neurological data not only show that satiation neutralizes the prior positive affective value of the stimuli (e.g., O’Doherty et al. 2000), but also that over-satiation leads to aversion (e.g., Small et al. 2001). How a pre-experience of, for example, thirst when currently quenched would be manifested is not readily grasped. Arguably, semantic prospection, and not necessarily a first person pre-experience of a forthcoming dehydration, produces the adequate incentive to fill up the water bottle when a thirst is slaked. Note that this is not equivalent with an a priori impossibility of the use of episodic prospection in any of such planning tasks, but rather it means that an anticipatory behavior is executed when satiated is not a decisive criterion for episodic forethought. In the search for behavioral criteria, an indisputable sign of episodic pre-experience appears to be unattainable. However, experiments based on a self-control design, increases the likelihood of measuring the outcome of a struggle between drive states related to the present and the future. A self-control experiment differs from a satiation experiment in that drive states are induced and present instead of reduced and absent. Having contesting drive states offers an opportunity of the future oriented one being related to a pre-experience, as opposed to the satiation context where pre-experience is a less probable process. If pre-experience of some aspects of the possible future evokes the motivation to act towards this future, then this poses a case of first person episodic relation to the upcoming event.

Self-control experiments aimed to elucidate planning skills need some specific design requirements. These must

be scrutinized in order to expound the behavioral criteria pursued in this study. First of all, to ensure that the self-control setting offers competition between *different* desires, the stimuli in the choice situation must represent different kinds of rewards. The immediate reward must be qualitatively distinct from the future one; otherwise the outcome of the choice would only be an expression of inhibitory strength and not of the ability to distinguish the future oriented drive from the present oriented one. And of course, both rewards must be highly valued but different in quantity, with the lesser amount in the immediate situation.

Secondly, it is pivotal that the cuing occurring in the self-control setting is thoroughly controlled; otherwise associative learning or immediate need planning cannot be precluded. To understand the role of cuing in planning, it should first be realized that cognition resulting in prospective behavior is cued, externally or internally, in the current situation, otherwise it would not be the result of deliberate planning, but of chance-like mental processes (haphazardly popping up in the head). On the other hand, to qualify as planning for the future, the prospective behavior must not be instigated by a current drive state or some present stimuli that might stand in an associatively learned relation to the future event (e.g., Tulving 2005). This distinction between cued and learned relations can be clarified by highlighting the difference between association and associative learning. Association, as in associating something to something else, is an everyday term that potentially includes a wide variety of cognitive mechanisms involved in cuing processes. Associative learning, on the other hand, is a term describing learning mechanisms characterized by an arbitrary connection between stimulus and reward, a link that is, so to speak, blindly learned through reinforcement. Another essential and related point is tied to the status of the drive state in the planning situation. Planning takes place in the present and is always governed by a motivation. It is the way in which this motivation is evoked that should make the difference between being an immediate and a future planner. A cue to a future event might eventually result in a drive state, for example a craving, that in turn evokes a motivation to plan, however, it is not the drive state per se that evokes the prospection, rather it is the other way around. This distinction is crucial: creatures unable to plan for future drives should be incapable of representing the future in a way that evokes a drive related to it. In fact, the emotional information received from a pre-experience of a potential future seems to constitute one of the key functions of an episodic prospective system (e.g., Gilbert and Wilson 2007; Ainslie 2007; Atance and Meltzoff 2007). Given the above distinctions, it is recognized that the motivation for planning for future needs not only might, but must, be triggered, and that this trigger may very well be a current drive state connected to the future

event as long as this is a result of some form of forethought. This leads to the other imperative requirement for a self-control setting designed to study planning abilities: the stimuli related to the future event must be controlled for not having an associatively learned connection to the upcoming reward. If there does not exist an associatively learned link, then the potential cuing should be compatible with true planning for future needs.

As mentioned, there is probably not a single test providing both the necessary and sufficient elements to falsify the Bischof–Köhler hypothesis. A properly designed and well-controlled self-control setting, most certainly evokes a drive towards the stimulus of the present reward, and it is highly likely that the future oriented stimulus also induces a drive that offers competition. However, it is possible that only the future related drive is a motivation to plan, instigated by a rule-based knowledge of an upcoming event instead by a pre-experience (given that a motivation to plan is not viewed as a pre-experience). An interesting consequence is that positive results from such experiments would clearly indicate planning for future needs, without falsifying the Bischof–Köhler hypothesis.

Further investigations of the episodic content should be related to the term “flexibility” in the Bischof–Köhler hypothesis. An operationalizable distinction between episodic and semantic prospection is that the former deals with the particularities of the upcoming event, whereas the latter is only concerned with regularities (Suddendorf and Corballis 2007). An intuitive test would be to create future situations with each having a unique character, and then control for whether the subjects take into account the exclusive features of each future situation when planning. However this is a non-viable experimental construction, offering a low degree of control. The difficulties are numerous, but the most severe would be to inform non-linguistic subject in a controlled fashion about the unique upcoming event, and further to ensure that this information has been interpreted in the intended way. However, even if episodic prospection proves its strength in relation to unique events, it could still be tested with repeated future events with the same re-occurring content. Instead of manipulating the future events, the current situation in which the planning takes place could be altered so that it relates to the particularities of the future event, for example, letting subjects select between functional and non-functional novel tools that could potentially be used on a familiar future problem, where the potential functionality must be mentally compared with the particularities of the future situation. In other words, an investigation, in the planning situation, of the sensitivity to unique particularities linked to features of the upcoming event, would provide robust insights into the ability to foresee the particularities of a future episode.

Some recent studies on future oriented cognition in corvids and primates challenge the Bischof–Köhler-hypothesis to some extent. Two studies on Western scrub-jays (*Aphelocoma californica*) show that these birds adapt present actions to a future need without reference to a current drive state (Correia et al. 2007; Raby et al. 2007). These studies are based on the satiation-setting: controlling for the lack of the specific drive state that the anticipatory action is aimed at. The results indicate a skill for planning for future needs. However, the planning behaviors of the scrub-jays have been proposed to be specific adaptations to the caching context rather than constituting a flexible skill of the kind seen in humans (Gilbert and Wilson 2007; Premack 2007; Suddendorf and Corballis 2007). True or not, the prospective abilities of corvids must indeed differ vastly in phylogenesis from that of humans due to the considerable distance to our last common ancestor (e.g., Emery 2006). This makes the data highly interesting, as they provide a good example of how complex cognitive traits might result from convergent evolution in distantly related species.

Nonetheless, to gain deeper understanding of the particular evolution of the human planning ability, studies of primates are necessary. It has been revealed that bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*) can select and save a tool for later use (Mulcahy and Call 2006), and that future states of thirst may affect present food choices in squirrel monkeys (*Saimiri sciureus*) (Naqshbandi and Roberts 2006). These studies remain controversial, as the drive states of the subjects are not controlled for (Correia et al. 2007; Raby et al. 2007; Shettleworth 2007; Suddendorf 2006; Suddendorf and Corballis 2007) and associative learning is not sufficiently excluded as an explanation of the results (Correia et al. 2007; Raby et al. 2007; Shettleworth 2007; Suddendorf and Corballis 2007). The study of Mulcahy and Call (2006) showed that great apes are capable of saving tools needed in a distant future. However, a control for the motivational state of the subjects was not included in these experiments (as opposed to the studies of the scrub-jays). It has been suggested that the subjects could potentially experience a desire for the reward throughout the experiment (Suddendorf 2006; Suddendorf and Corballis 2007). Therefore it is not considered clear whether the apes only anticipated the future need for the tool or if they also foresaw their future motivational state. Furthermore, some argue that it is not possible to exclude associative learning because the same tools rewarded the subjects throughout the experiment (Suddendorf and Corballis 2007).

Due to these considerations, it is still an open question whether primates other than humans possess the multicomponent skill for future planning. Consequently, the evolutionary history of one of our most significant cognitive skills is largely unearched. To begin to resolve the question whether great apes are cognitively capable of planning for

future states in a way similar to that of humans, it must be shown that they can go beyond the satisfaction of immediate drives, and it must be demonstrated that subjects do not merely employ associative learning or semantic prospection instead of episodic prospection in a planning task (Correia et al. 2007; Gilbert and Wilson 2007; Gulz 1991; Köhler 1921; Raby et al. 2007; Shettleworth 2007; Suddendorf 2006; Suddendorf and Busby 2005; Suddendorf and Corballis 1997, 2007; Tulving 2005).

The following series of experiments adhere to the afore-described behavioral criteria, and thereby not only addresses the methodological concerns raised towards the previous planning study conducted on great apes (Mulcahy and Call 2006), but also extends the investigations further. To properly tackle some of the intriguing issues of planning skills in non-human primates, we engaged two chimpanzees (Linda and Maria Magdalena) and one orangutan (Naong) in a series of experiments. The aim was to give an answer to: whether great apes meet the above-mentioned cognitive requirements in planning tasks; whether they are capable of out-competing a current drive in favor of a highly delayed reward and; whether they are able to act towards a future by pre-experiencing it mentally rather than relying on associative learning or semantic rule following? The study included four experiments, divided into a baseline, a self-control test, an association control and pre-experience test.

Experiment 1: baseline

This experiment tested the apes' selection of objects in a choice situation, presenting an opportunity to get hold of a tool leading to a delayed reward at a location not visible from the selection site. The experiment was divided into two phases. The first phase included tool use training and a setting that was intended to inform the subjects about the reoccurrence of the reward. The second phase was the actual testing. Before the experiment was initiated, a control was conducted on the experimental procedure and on parts of the key materials.

Methods

Subjects

Two chimpanzees and one orangutan housed at Lund University Primate Research Station, Furuvik Zoo (Sweden) participated in the main experiment. The two female chimpanzees, Linda and Maria Magdalena, were 22 and 6 years old, respectively. The male orangutan Naong was 12 years old. Linda, who was wild-caught in Liberia, was partially hand raised, while the other chimpanzee and the orangutan were mother raised in captivity. The chimpanzee subjects

shared their enclosure with three other chimpanzees. One of these was a male at 28 years of age, in alpha position. The other two were females, one adult at 24 years of age and one infant (of Linda) at the age of 2. The orangutan shared the enclosure with a 20-year-old female. The two adult chimpanzees and the female orangutan served as control subjects in the control for biases, in the materials or the selection procedure in Experiments 1 and 4, but did not take any further part in the study.

All subjects were experimentally naïve when this study started. The subjects lived in their social groups and in their everyday indoor and outdoor enclosures during the experiment. They were not deprived of water or food. Water was accessible *ad libitum* in the enclosures.

Materials

A wooden box (19 × 15 × 36 cm) contained a transparent plastic bottle, accessible through a hole (2.5 cm in diameter) on top of the box. At the front of the box, a 15 cm high Plexiglas panel offered a view of the contents. The reward was half a liter of a highly favored fruit soup. To obtain the reward, a soft and transparent plastic hose was needed (70 cm in length and 4 mm in diameter). It was used as a straw to suck the soup up. The hose was placed on a wooden tray (75 × 45 cm), from which the subjects could select between this functional tool and three other distracter objects. The distracter objects were objects commonly used by the subjects in different enrichment activities and thus possibly associated with previous rewards. The distracters were a rope, a bamboo stick and a heavily knotted sling.

Procedure, design and control

The training phase was designed to let the subjects learn how to use the tool to obtain the large liquid reward, and to inform them about the reoccurrence of this reward. At the same time, the opportunity for associative learning was kept at a minimum by not allowing repeated training, with short intervals between the tool and the reward. A keeper demonstrated the plastic hose and its function by sucking fruit soup from the apparatus while a subject was observing from close range. Then the hose was extracted from the apparatus and handed to the subject. Subsequently, all three subjects spontaneously reinserted the hose into the apparatus and obtained the reward. The tool use training was restricted to this single trial. This was also the only occasion during the entire experiment series when subjects were immediately rewarded by acquiring the tool. Later, the baited apparatus was installed in a reward room to which the subjects were granted access without possessing any tools. This was done to create a possible incentive for possessing a functional tool in the future. This procedure was

repeated twice in a day. The day after having experienced these reoccurrences, subjects were presented with the tray containing the four objects out of which one, the hose, was functional for obtaining the reward. Subjects were only permitted to select one of the objects. The training selection was made when the apparatus was visible but unattainable in the reward room. Subjects were not allowed into the reward room until 1 h had passed after their selection. All subjects selected the functional tool in the first training trial. This was the second time they ever saw the tool.

In the actual experimental task, the subjects were individually called inside a selection room, from where the reward room was not visible. A trial started, with the ape being offered to select one of the four objects from the tray. The tray was placed out of reach but within sight for approximately 4 s. Then it was slid towards the subject. To minimize potential cuing, the experimenter never looked at the objects before the ape made the selection, and fixed his or her gaze at a point slightly above and behind the head of the subject. As soon as the subjects selected an object by either touching it or its immediate area, the tray was removed to avoid attempts to acquire more than one object. The objects were located approximately 10 cm from each other resulting in unambiguous choices. The position of the objects was pseudo-randomized between trials. After the selection procedure, the subjects returned to the daily enclosure with the selected object. This enclosure was shared by other group members, something that forced subjects to keep track of and sometimes defend their tool (this set up was of importance for Experiments 2 and 3, as will be returned to). Seventy minutes later the apparatus was installed and the subject gained access to the reward room. A trial ended as soon as the subjects obtained the reward, or when 5 min had passed. After the reward was finished, the tool was taken away from the subject. Then the subjects were urged to return to the enclosure from where they could observe the immediate removal of the apparatus. Prior to every trial, subjects had the opportunity to observe that no apparatus was installed in the reward room before they were called inside the selection room, since the bars dividing the daily enclosure and the reward room offered full view. Fourteen trials were performed on each subject. Two sessions, including one trial each were conducted per day. The complete experiment was not carried out on seven consecutive days, but was divided into three periods with 2 days of testing on two occasions and 3 days of testing in the last period. Each testing period started with 1 day when the reward reoccurred twice without the subjects having the opportunity to possess any appropriate tools.

Before the testing phase, a control for potential selection biases was conducted. This was done with the aforementioned three control subjects, two chimpanzees and one orangutan. Using different individuals in the control than in

the experiment prevented unwanted learning. The chimpanzees had shared the same environment for the last 20 years, the orangutans for the last 3, and they were all naïve to the function of the tool as they had not received training on the apparatus. The control subjects were offered the opportunity to select from the identical board and objects as in the experiment. As in the experiment, the selection procedure was restricted to the selection room. Control subjects were offered the choice three times a day for a total of 14 times. There were no significant deviances from a chance distribution of choices (multinomial test). There were no significant choices of any of the specific objects (Fisher's exact test). The most selected object was the bamboo stick, however, not significantly. The chimpanzee male refused to select on two occasions and the chimpanzee female refused selection in one trial, this was conservatively calculated as hose selections. All together, the chimpanzees selected the functional tool three times each, and the orangutan selected it twice. From the absolute numbers of actual selections (excluding the refusals) a tendency, which might be interpreted that the familiar objects evoked a somewhat greater interest than the functional tool, can be derived. Importantly in this control the functional tool was not selected significantly more often than other items. We concluded that the specific objects did not evoke significant biases that would influence the main experiment.

Results

Out of the 14 trials performed, one chimpanzee (Linda), and the orangutan selected the functional tool in 100% of the trials. The other chimpanzee selected the functional tool in 13 of the trials. Their choices differed significantly from chance (Fisher's exact test, Linda and Naong $P = 0.0002$; Maria Magdalena $P = 0.0013$). One chimpanzee (Linda) brought and used the tool after the delay in 11 trials, while in the other three cases the tool was misplaced by her infant during the delay period (trial 3, 9 and 10). The other chimpanzee succeeded in bringing the tool in 12 trials. Her tool losses were also recorded as caused by Linda's playing infant (trial 5 and 10). The orangutan Naong brought the functional tool in 11 trials. In two of the unsuccessful trials he actually did bring the tool, though in a non-functional state as it was damaged from being carried in his mouth (trial 1 and 8). In the third case, the tool was dropped outside the enclosure (trial 11). All subjects obtained the reward when possessing the tool.

Discussion

Consistent with the findings of a previous study (Mulcahy and Call 2006), the results of this experiment show that great apes are able to select and save a tool for future use.

Furthermore, the results show that great apes can select the correct tool in a location with no visual cuing to the future reward site. In the study of Mulcahy and Call (2006), it was demonstrated that apes were able to select a tool in the absence of the reward. This selection was conducted at the same site as the reward reoccurred. A selection at a different location with such a long delay has not been tested before (note however Mulcahy et al. 2005, for shorter delays) and is viewed as an important achievement in a planning context indicating a profound cognitive detachment from the perceptual stimuli (e.g., Tulving 2005). Furthermore, it should be noted that subjects were able to observe the absence of the apparatus, both before they were called inside the selection room and during their time of waiting with the tool. This means that they could not have selected a tool in reference to an existing reward at the reward site and that they could not have selected it to obtain an immediate reward after leaving the selection room. An associatively learned link between the tool and the reward is less likely due to the lack of short interval repetitions between the tool and the reward. However, the question of association is empirically addressed in Experiments 3 and 4. Another important aspect that extends this study beyond the previous one (Mulcahy and Call 2006), is that the subjects shared their waiting area with other individuals, instead of spending the delay time alone in a designated room. This presumably added a cognitive load to the subjects, not only when it comes to keeping the tool from getting lost, but also in the context of all the attention grabbing episodes that occur in ape enclosures in zoos. Among other things, this implies that subjects were not constantly cued by the presence of their tool. In other words it is unlikely that the desire for fruit soup was the predominant drive state during the delay. Being able to cope with such distracting factors is often relevant for future planning. The results of this experiment suggest behaviors based on advanced future oriented cognition.

Experiment 2: self-control in the face of a future reward

This experiment tested the ability to suppress the selection of an immediate reward in favor of a tool that would lead to a larger reward in the future. To show whether the subjects truly plan for a future need, they must override a motivation to satisfy a drive immediately in favor of a motivation to satisfy a different kind of drive in the future.

Methods

Subjects

The subjects, their surroundings and further conditions were identical to those described in Experiment 1.

Materials

All the materials were identical to the materials in Experiment 1, with one crucial exception. In the array of the above-described selectable objects, a favorite fruit of the subjects was included. In different enrichment activities, not related to this experiment, the zookeepers have established the favorite fruit to be grapes for all three subjects. Grapes had the status of a special treat for these subjects.

Procedure and design

The setup was identical to that of Experiment 1 (not including the training phase), except that the favorite fruit was established and added to the array of possible choices to evoke a strong immediate motivation that would compete with the future reward. In other words, subjects were called inside the selection room and offered a choice similar to that in Experiment 1, but with their favorite fruit included among the immediately selectable objects. As in the previous experiment, only one choice per trial was allowed and consistently, the time of delay was 70 min. In the context of this experiment, it should be noted that sometimes it is assumed that the steep discounting of the value of a future reward seen in animals results from the high risk of postponing a reward. To decline an immediate reward might lead to not obtaining any reward at all. By exposing subjects to the risk of tool loss due to group interactions, this factor was taken into account. Fourteen trials were conducted on each subject.

Data analysis

The expected choice of an animal not able to plan for the future is the immediate favorite fruit. Hence, the analysis of the data is based on this expectation. The question of interest in this experiment is which of the two represented reward types does the subject chooses: the immediate reward or the delayed reward. The distracter objects introduced in Experiment 1 were kept in Experiment 2, only to minimize the change in set up, avoiding any unwanted biasing that might have occurred by removing them.

Results

In 14 trials, one chimpanzee (Linda) selected the functional tool 8 times, the other chimpanzee selected it 11 times, and the orangutan 9 times. This is significantly above, expected choice of the immediate satisfaction (Fisher's exact test, Linda $P = 0.0019$ and Naong $P = 0.0006$, Maria Magdalena $P = 0.00003$). All subjects selected the fruit when they were not selecting the tool. Maria Magdalena and Naong both selected the tool in their first trial and Linda in her second.

Maria Magdalena selected the grape in trials 2, 7 and 9. Naong selected the grape in trials 3, 5, 8, 10 and 13. Linda selected the grape in trials 1, 4, 5, 7, 8 and 13. The orangutan brought and used the tool in all the trials it was selected. Maria Magdalena did not succeed in bringing the tool in two trials (trial 1 and 8). One of the tool losses was caused by the playing infant. The other loss was a result of Maria Magdalena avoiding entering the room where she placed the tool, most likely because of the presence of the agitated dominant male. Linda did not bring the tool in four trials (trial 2, 3, 9 and 12). One of the losses was not observed. All of the other three got lost in everyday fighting.

Discussion

Subjects not able to plan for future needs are expected to choose the immediate favorite fruit reward, because they would be unable to represent the future fruit soup and the related need-state of satisfying the desire for it. It should also be noted that the tool lacks function until 70 min later, which arguably constitutes a considerable temporal distance for a non-planner. Moreover, selecting the tool does not eliminate any potential immediate craving for fruit soup and obviously it does not eliminate the craving for the grape. Therefore, selecting the tool without a reference to the future reward would appear maladaptive. The favorite fruit differed not only in quantity but also in quality from the future liquid reward. This removes the theoretical possibility that an act of self-control is governed by an immediate drive evoked by the grape (declining one grape in favor of more grapes). The level of performance in this experiment seems to be above or comparable to that of adult humans, both regarding to the time of the delays as well as to the percentage of exhibited self-control (Forzano and Logue 1992). This great ape ability in food related self-control tasks is also confirmed by Rosati et al. (2007). The hypothesis of non-human impulsivity is seemingly not true for great apes in a planning context. These results strongly suggest that great apes are able to make choices favoring future needs in direct competition with immediate drive states.

Experiment 3: Controlling for associative learning

This experiment was designed to rule out that the subjects merely ascribe the tool an intrinsically high value detached from its future function. Such an association could explain the results in Experiments 1 and 2 without assuming future planning capacities. In other words, if the tool evoked an immediate craving in the same sense as the grape, then selecting the hose would reduce this drive state and consequently not be part of a planning behavior. This experiment controlled for such a possibility.

Methods

Subjects and materials

The subjects, their surroundings and further conditions were identical to those of the above-described experiments. The materials were the same as in Experiment 2, including the type of favorite fruit.

Procedure and design

As in Experiment 1, the subjects were given the choice between three non-functional tools and one functional tool. When the subjects had selected the functional tool, as expected, and thus had it in its possession, they were immediately offered a new choice including a second copy of the functional tool and a favorite fruit (in effect making the choice identical to the one in Experiment 2). Every other procedural aspect of this experiment was the same as in the previous experiments. Fourteen trials were conducted on each subject.

Data analysis, results and discussion

If subjects merely attribute a strong positive value to the tool as such, then the result in the second pairing should mirror the outcome of Experiment 2. However, if instead the tool was valued as an instrument used for obtaining the future reward, then the favorite fruit would be the expected choice. The tool is a means to an end, and the future reward will not grow larger if more tools are selected. By selecting the grape in the second presentation, the subject maximizes the rewards. All three apes selected the fruit on each of the 14 trials. The results significantly deviate from chance (Fisher's exact test, $P = 0.006$), and do not mirror the results in Experiment 2. Note that this calculation is conservative, given that the results from Experiment 2 would make the tool the expected choice. This excluded associative learning as an explanation for the results in Experiments 1 and 2. This does not suggest, however, that the animals lacked positive associations in relation to the tool, just as humans probably do in relation to useful tools. Rather, it means that the association is not of the arbitrary nature that would be expected from mechanisms of associative learning.

It would not be suboptimal to occasionally choose the tool more than once, because the subjects did lose their tools in various group interactions in Experiments 1 and 2 at an average of 20% of the times per subject. In this experiment, the tool losses were at a similar level except for the orangutan (Linda 3 losses, Maria Magdalena 2 losses and Naong 0 losses). The heavy bias towards the grape in the second selection is most likely explained by the strong

craving, the grape actually evoked in these subjects. It should be noted that the results of Experiments 2 and 3 are interrelated according to the status of the immediate reward. A less preferred immediate reward would probably yield better results on the self-control task and less clear results in the association control.

Experiment 4: pre-experiencing future particularities?

This experiment addressed whether the apes pre-experience their future tool actions. In the previous experimental choice situations, there is a chance that subjects might have known that the apparatus will reappear in the future, without pre-experiencing this future scenario. This experiment investigated such a possibility by introducing novel tools never encountered by the subjects before.

Methods

Subjects

The subjects, their surroundings and further conditions were identical to those described for Experiment 1, except that the experimental subjects did not share the enclosure with each other during the delays to preclude unwanted learning about the novel tool.

Materials

The selectable objects used in this experiment differed from the ones in the previous experiments. For each of the 12 trials, a different set of selectable objects was displayed. In each trial, the functional tool as well as two of the three distracter objects was novel to the subjects. See Table 1 for a description of the novel tools and distracter objects. In all the trials, the choice also included a familiar bamboo stick previously associated with food acquisition (honey extraction).

Procedure and design

In each trial in this experiment, subjects selected among three novel objects, and a fourth object linked to food acquisition (though non-functional in this task). Out of the three novel objects, only one could function as a tool for obtaining the future reward. These tools appeared (to a human) as highly dissimilar from the soft, curled, and transparent hose used in previous experiments. The subjects were only given the opportunity of visual inspection of the objects. To avoid social learning, the subjects were not allowed to observe the others selecting, saving, or using the tool. An experimenter rotated each object for an equal

Table 1 The table describes the novel tools and the distracter objects presented for the subjects in Experiment 4

Trial	Novel functional tool	Distracter 1	Distracter 2
1	White plastic pipe (40 cm in length, 16 mm in diameter)	Blue plastic car	Feathery part of a cap
2	Multicolored rubber “twin” hose (48 cm in length, 2 × 5 mm in diameter)	Small teddy bear	Transparent ruler
3	Square hollow aluminum frame (45 cm in length, 4 × 14 mm in circumference)	Multicolored necklace	White electric cord
4	Multicolored 90° bent pipe (45 + 10 cm in length, 16 mm in diameter)	White nylon rope	Metal belt buckle
5	Black thick rubber hose (41 cm in length, 20 mm in diameter)	Green-black screwdriver handle	Long bent hay straw
6	Triangular hollow wooden frame (45 cm in length, 3 × 15 mm in diameter)	Discarded wrist watch	Orange nylon rope
7	Hollow bamboo stick (43 cm in length, approx. 15 mm in diameter)	Yellow plastic toy spade	Black cloth
8	Orange rubber hose (55 cm in length, 5 mm in diameter)	Cardboard piece with banana picture	Metal wire
9	Beige “flat” textile hose (45 cm in length, 20 mm in diameter when “open”)	Elongated Plexiglas piece	Green pencil
10	Metal pipe with spiral form at end (47 cm in length, 16 mm in diameter)	Blue nylon rope	Square piece of oak wood
11	Black square hollow plastic frame (40 cm in length, 4 × 10 mm in diameter)	Small plastic drinking glass	Metal rod
12	Gray grooved plastic hose/pipe (58 cm in length, 10 mm in diameter)	Brown bootlace	White–blue toy shark

Note that the fourth selectable object in all 12 trials was the familiar (non-hollow) bamboo stick

amount of time and at slow speed in front of the ape. The functional tool was rotated as the second or the third object in order to minimize possible biasing effects due to the first or last position. To preclude potential gaze cuing, the experimenter focused his or her gaze behind and slightly above the subject, without having eye contact or gazing directly at the objects. A tool was used only once in a single trial because its novelty was lost after one use.

Control

A control was conducted to find potential biases for selecting the novel functional tool without the relevant connection to the reward apparatus. This control was made with the three apparatus naïve subjects that took part in the control in Experiment 1. The control selections were conducted in the selection room with materials identical to those of the main experiment. Consequently, 12 trials were conducted per control subject. As in the control of Experiment 1, a subject carried out three control trials a day. The novel functional tool was not selected significantly above chance (Fisher’s exact test). The male chimpanzee selected the functional tool in two trials (trials 4 and 5). He refused selection in the last four trials (probably indicating lack of interest in the objects). The female chimpanzee selected the

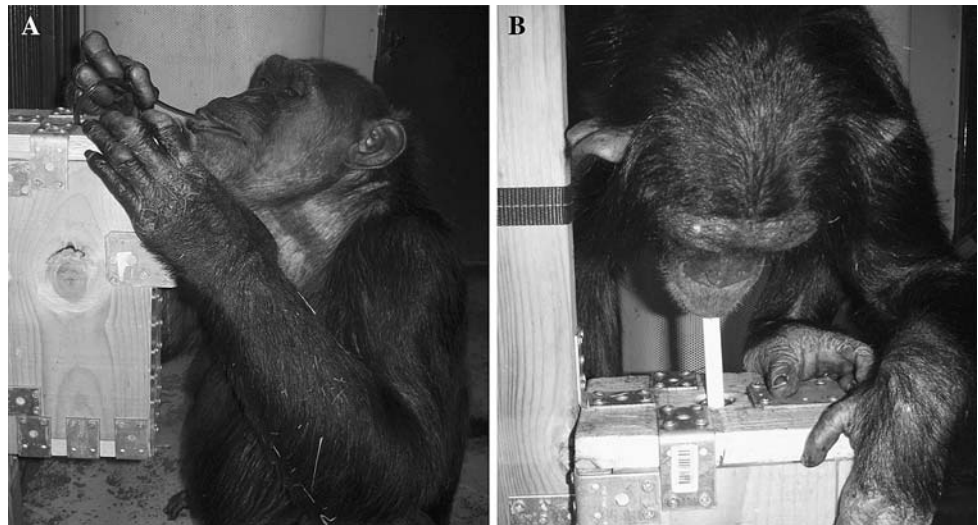
functional tool in three trials (trials 2, 8 and 12). This was also true for the female orangutan that selected the tool in trials 2, 8, and 10. All three control subjects chose the same distracter object in three trials (the blue plastic car used in trial 1, the multicolored necklace used in trial 3 and the discarded wrist watch used in trial 6). In trial 8, two of the control subjects selected the functional tool. Based on these findings, we concluded that potential biases were at an acceptable level for using the objects in the main experiment.

Results

The orangutan selected the functional tool in 11 of the 12 trials (failed in trial 9). One chimpanzee (Linda) selected the functional tool in ten trials (failed in trial 7 and 9) and the other chimpanzee in nine trials (failed in trial 6,7 and 9). The novel functional tool was selected significantly above chance by all three subjects (Fisher’s exact test, Naong $P = 0.003$, Linda $P = 0.012$, Maria Magdalena $P = 0.039$).

In the successful choices, the subjects brought the tool to the reward room after the delay and used it appropriately with no observable hesitation (see Fig. 1). Furthermore, they did not try to use the non-functional tools in the trials where such were selected.

Fig. 1 Chimpanzees are obtaining the liquid reward with different tools. Linda (a) is using the hose that constituted the functional tool in the first three experiments. Maria Magdalena (b) is using the hard pipe that was displayed in trial 1 in experiment 4. Note that the hose is utilized from below with the subject sitting on the floor while drinking, whereas the pipe requires a different drinking position



Discussion

The results of this experiment indicate that the apes pre-experience the future tool function and its use. This strengthens the likeliness that episodic prospection is involved in the tool selection tasks in this study. Stimulus generalization does not offer a sufficient explanation because the subjects were sensitive to the functional aspects of the tools rather than to arbitrary features. The alternative functional tools in this experiment markedly differed from the original tool used in the previous three experiments, and several of the distracters shared features with the original tool. The two features common in the functional tools were a length above the minimum required for reward retrieval (approximately 38 cm), and holes in both the ends. However, these features notably varied from the original tool. Both the longest and the shortest of the novel tools were shorter than the original (12, respectively; 30 cm shorter). The holes in the novel objects did not differ only in diameter (up to 16 mm larger) but also in shape (round, square and triangular) and numbers (two holes at each end in the tool in trial 2). Furthermore, several of the distracter objects carried features that were present in the original tool (see Table 1), for example, transparency (trial 2, 9, 11) or thin elongation (trial 3, 4, 5, 6, 8, 10, 12). Given the varied nature of the shared features in the functional tools, and that the original tool shared features with several distracters, it is fair to assume that the results show a tool selection based on the functional properties. This is in line with Call (2006), who noted that apes are better in understanding the causal properties of the physical world than in associating arbitrary stimuli and responses.

A more complicated question is whether these results reflect semantic or episodic prospection. It could be argued that even if subjects selected the tool because of its function, they might have followed a semantic rule instead of

pre-experiencing the reward retrieval situation. However, it cannot be argued that the actions towards the upcoming event are governed by semantic prospection solely because the future target event is repeated through the trials. The selection situation includes particularities that must be compared with the upcoming event, requiring unique comparisons in each trial. Nevertheless, it cannot be entirely excluded that semantic rules offer the main mechanism in this kind of single trial generalizations of non-discrete features to future functions; however, the concept of semantic prospection still seems to be too vague to offer guidance. Given our current understanding, the results in this experiment indicate pre-experiencing of the particularities of a future event.

The lack of observable hesitation in the tool use was striking and would suggest a high fidelity in the envisioning of the function and the necessary manipulations.

General discussion

In several important aspects, this study extends beyond previous knowledge about prospective cognition in great apes (Mulcahy and Call 2006). It shows that great apes are capable of acting towards a future state although experiencing a strong current and competing drive. Self-control in relation to such highly delayed events as described here is till date not reported for non-human animals. Furthermore, it is shown that great apes can generalize a function from a completely novel object to a future use. This ability seems paralleled only by human envisioning of a future event. Some of the crucial data in the study make it unlikely that the behaviors surrounding the tools should be a result from associative learning or semantic rule following, rather than from actual planning. It is also shown that great apes are capable of selecting objects needed for a much-delayed

future in a different and not currently perceived location. Furthermore, it is demonstrated that great apes are able to cope with planning tasks under the presumably high cognitive load, produced by taking part in everyday social life. When amalgating the experiments of this study, it is strongly suggested that great apes can plan for the future (see Table 2 for overview of the experimental results).

There is a widespread tendency to use associative learning in explanations of non-predisposed animal behavior. Such explanations do not account for the key behaviors exhibited by the subjects in this study. Only once during the study did subjects obtain the tool with an immediate accessible reward present, and this was on the first occasion they used the hose. Thereafter the delay between acquiring the tool and the occurrence of the attainable reward lasted for at least 1 h. Furthermore, the subjects did not always obtain the reward even if the correct tool was selected, because the tool sometimes got lost in various group interactions during the delay (a mean of approximately 20% of the times per subject). Such circumstances are not readily compatible with associative learning. Examples of associative learning from single occasions are few and seemingly connected to species-specific predispositions such as innate defense behaviors (Bolles 1970) or preparedness (Seligman 1970) (like the development of fear of snakes or specific food avoidance when being nauseated). It appears invalid to assume these, or similar, mechanisms to be at work in this series of experiments. The exercise of self-control is an act of overriding hardwired impulses, and it would require extensive training, if at all possible, to associatively learn the level of self-control exhibited by the subjects. Obviously such training was not given. And, if selecting the tool instead of the favorite food was actually a result of training, the subjects would not have selected the tool in their first or second trial and there would have been a visible learning curve in the data. If there was an associatively learned connection between the plastic hose and the future reward, the tool would carry an intrinsic value detached from cognitive considerations about possible future events. To explain the outcome of Experiment 2 in such associative learning terms, this value would have had to be even greater than

that of the favorite fruit. Experiment 3 clearly and decisively demonstrates that this is not the case, and thereby also shows that associative learning has not been at work in Experiment 1. Experiment 4 does not constitute fertile ground for associative learning mechanisms, because the tools and their functions were never learned but were completely novel and highly dissimilar from the original, as well as from each other.

Another possible explanation would be that the results reflect semantic prospection. However, the current knowledge about semantic prospection is scarce. The area appears to be uncharted and does not rest on a direct empirical ground. When further developed, the concept might very well prove its explanatory value. Nevertheless, given the present understanding and definition it seems likely that the result in at least Experiment 4 would be incompatible with semantic prospection.

When turning to the potential status of the needs in this study, it is worth pointing out that it is improbable that immediate needs governed the subjects' choices in the successful trials. This would have required that all the subjects in 54 trials experienced a desire for fruit soup already when entering the selection procedure. Desire for fruit soup is rather specific and seemingly far from the expressions of more common basic biological needs (any general thirst could have been slaked at any time by the drinking facilities in the enclosures). Considering all feasible drive states that could have been experienced by the subjects at any given moment, it would arguably yield an extremely low chance that the immediate need in the moment prior to the selection was that of fruit soup. The chances that a potential desire is evoked during the selection moment seem much greater. And, such a trigger is not always equivalent with a trigger that evokes an immediate need, even less so if the stimuli are not associatively learned. Although previously discussed, a brief recapitulation might be appropriate to further appreciate this point. Experiments 2 and 3 were designed to create a strong immediate desire for the instantly available favorite fruit. It is hypothesized that an animal mentally stuck in the present is unable to circumvent the immediate reward in favor of something occurring

Table 2 The table shows an overview of the number of appropriate responses (from the view of a planner)

Subject	Experiment 1 Selecting the functional tool (max $n = 14$)	Experiment 2 Selecting the functional tool (max $n = 14$)	Experiment 3 Selecting the favorite fruit (max $n = 14$)	Experiment 4 Selecting the novel functional tool (max $n = 12$)	Total experiments (max $n = 54$)
Naong (<i>Pongo abelii</i>)	14	9	14	11	48
Linda (<i>Pan troglodytes</i>)	14	8	14	10	46
Maria Magdalena (<i>Pan troglodytes</i>)	13	11	14	9	47

It would be difficult to collapse the statistics from all four experiments, though it is noteworthy that all subjects perform the appropriate key behavior in more than 85% of the total of the trials

in the future. The theoretical consequence is that any potential immediate needs related to fruit soup are instead shifted towards the instant reward. Unless, the stimulus related to the future reward evokes a drive that can be satisfied by attaining the stimulus itself, and thereby in consequence making the experimental situation a choice between two immediate rewards. Experiment 3 excludes such a possibility from this study. Another viable alternative to select the future oriented stimulus is that a prospection evokes a potential craving towards the future reward, that is anticipating the mental state of a future need.

The results of this study entail that capacities central to humans evolved much earlier than previously believed (e.g., Noble and Davidson 1996; Macphail 1998; Osvath and Gärdenfors 2005; Suddendorf and Corballis 1997). Furthermore, they imply that apes use cognition described as self-conscious when exhibited by humans. The results fit well with the neurological data indicating an experienced inner mental world in chimpanzees (Rilling et al. 2007). The findings are interesting when considering the study of extant great apes as well as when discussing the evolution of human cognition. For example, the advanced social strategies displayed by chimpanzees (e.g., de Waal 1982), or the chimpanzee customs surrounding warfare, hunting or tool use in the wild (e.g., Boesch and Boesch-Acherman 2000), might be given richer interpretations than accepted before. When it comes to human cognitive evolution the data support the theories claiming that the skill for future need planning phylogenetically precedes language and even facilitates the evolution of the communicative system of humans (Osvath and Gärdenfors 2005; Suddendorf and Corballis 1997).

It cannot be claimed that the planning skills of humans are identical to those of the other great apes, but rather that there does not seem to exist a profound evolutionary discontinuity in the ability to foresee future needs. To gain further understanding of the phylogeny of planning skills, and to get deeper insights into the abilities that are at play in this specific study, it would be fruitful to conduct a close analog of this series of experiment on gibbons (the closest relatives to the great apes), on small children (in the development of prospection), and on representatives of the rare clinical group, lacking episodic abilities (still having intact semantic systems). Additionally, in the interest of the broader endeavor to understand the prospective skill as a biological and cognitive phenomenon, it would be productive to compare the performance of distantly related species on tasks similar to this study.

Acknowledgments We would like to thank the members of the LUCS-seminar and Josep Call, Frans de Waal, Daniel Haun, Tomas Persson, Endel Tulving and Staffan Ulfstrand. We are especially grateful to Ing-Marie Persson at Furuviik Zoo.

References

- Ainslie G (1974) Impulse control in pigeons. *J Exp Anal Behav* 21:485–489
- Ainslie G (2001) *Breakdown of Will*. Cambridge University Press, Cambridge
- Ainslie G (2007) Foresight has to pay off in the present moment. *Behav Brain Sci* 30:313–314
- Andreassen NC, O’Leary DS, Cizadlo T, Arndt S, Rezaei K, Watkins GL, Ponto LL, Hichwa RD (1995) Remembering the past: two facets of episodic memory explored with positron emission tomography. *Am J Psychiatry* 152:1576–1585
- Atance CM, Meltzoff AN (2007) How developmental science contributes to theories of future thinking. *Behav Brain Sci* 30:314–315
- Atance CM, O’Neill DK (2001) Episodic future thinking. *Trends Cognit Sci* 5:533–539
- Atance CM, O’Neill DK (2005) The emergence of episodic future thinking in humans. *Learn Motiv* 36:126–144
- Beran MJ, Evans TA (2006) Maintenance of delay of gratification by four chimpanzees (*Pan troglodytes*). *Behav Process* 73:315–324
- Beran MJ, Savage-Rumbaugh ES, Pate JL, Rumbaugh DM (1999) Delay of gratification in chimpanzees (*Pan troglodytes*). *Dev Psychobiol* 34:119–127
- Boesch C, Boesch-Acherman H (2000) *The Chimpanzees of the Tai Forest: behavioural ecology and evolution*. Oxford University Press, Oxford
- Bolles RC (1970) Species-specific defence reactions and avoidance learning. *Psych Rev* 77:32–48
- Buckner RL, Carroll DC (2007) Self-projection and the brain. *Trends Cognit Sci* 11:49–57
- Byrne R (1995) *The thinking ape: evolutionary origins of intelligence*. Oxford University Press, Oxford
- Call J (2006) Descartes’ two errors: reason and reflection in the great apes. In: Hurley S, Nudds M (eds) *Rational animals*. Oxford University Press, Oxford, pp 219–234
- Carlson SM, Moses LJ (2001) Individual differences in inhibitory control and children’s theory of mind. *Child Dev* 72:1032–1053
- Christoff K, Ream JM, Gabrieli JDE (2004) Neural basis of spontaneous thought processes. *Cortex* 40:623–630
- Clayton NS, Dickinson A (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395:272–274
- Clayton NS, Dickinson A (1999) Scrub jays (*Aphelocoma coerulescens*) remember the relative time of caching as well as the location and content of their caches. *J Comp Psychol* 113:403–416
- Correia SPC, Dickinson A, Clayton NS (2007) Western scrub-jays anticipate future needs independently of their current motivational state. *Curr Biol* 17:856–861
- de Waal FBM (1982) *Chimpanzee politics: power and sex among apes*. Jonathan Cape, London
- Duckworth AL, Seligman MEP (2005) Self-discipline outdoes IQ in predicting academic performance of adolescents. *Psychol Sci* 16:939–944
- Emery NJ (2006) Cognitive ornithology: the evolution of avian intelligence. *Philos Trans R Soc B* 361:23–43
- Evans TA, Beran MJ (2007) Chimpanzees use self-distraction to cope with impulsivity. *Biol Lett*, doi: 10.1098/rsbl.2007.0399
- Forzano LB, Logue AW (1992) Predictors of adult humans’ self-control and impulsiveness for food reinforcers. *Appetite* 19:33–47
- Fredrick S, Loewenstein G, O’Donoghue T (2002) Time discounting: a critical review. *J Econ Lit* 40:351–401
- Gardiner JM (2002) Episodic memory and auto-noetic consciousness: a first person approach. In: Baddeley A, Conway M, Aggleton J (eds) *Episodic memory—new directions in research*. Oxford University Press, Oxford, pp 11–30

- Gilbert DT, Wilson TD (2007) Propection: Experiencing the future. *Science* 317:1351–1354
- Gulz A (1991) The planning of action as a cognitive and biological phenomenon. *Lund Univ Cognit Stud* 2:1–187
- Ingvar DH (1979) “Hyperfrontal” distribution of the cerebral grey matter flow in resting wakefulness: on the functional anatomy of the conscious state. *Acta Neurol Scand* 60:12–25
- Köhler W (1921) Zur psychologie des schimpansen. *Psychol Forsch* 1:2–46
- Köhler W (1925) The mentality of apes. Penguin Books, London
- Maslow AH (1943) A theory of human motivation. *Psych Rev* 50:370–396
- Macphail EM (1998) The evolution of consciousness. Oxford University Press, New York
- Mischel W, Shoda Y, Rodriguez M (1989) Delay of gratification in children. *Science* 244:933–938
- Mulcahy NJ, Call J (2006) Apes save tool for future use. *Science* 312:1038–1040
- Mulcahy NJ, Call J, Dunbar R (2005) Gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) encode relevant problem features in a tool-using task. *J Comp Psychol* 119:23–32
- Naqshbandi M, Roberts WA (2006) Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): Test of the Bischof-Kohler hypothesis. *J Comp Psychol* 120:345–357
- Noble W, Davidson I (1996) Human evolution, language and mind: a psychological and archaeological inquiry. Cambridge University Press, Melbourne
- O’Doherty J, Rolls ET, Francis S, Bowtell R, McGlone F, Kobal G, Renner B, Ahne G (2000) Sensory-specific satiety-related olfactory activation of the human orbitofrontal cortex. *Neuroreport* 11:399–403
- Osvath M, Gärdenfors P (2005) Oldowan culture and the evolution of anticipatory cognition. *Lund Univ Cognit Stud* 122:1–16
- Premack D (2007) Humans and animal cognition: continuity and discontinuity. *Proc Natl Acad Sci USA* 104:13861–13867
- Raby CR, Alexis DM, Dickinson A, Clayton NS (2007) Planning for the future by western scrub-jays. *Nature* 445:919–921
- Ramseyer A, Pelé M, Dufour V, Chauvin C, Thierry B (2006) Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. *Proc R Soc B* 273:179–184
- Rilling JK, Barks SK, Parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR (2007) A comparison of resting-state brain activity in humans and chimpanzees. *Proc Natl Acad Sci USA* 104:17146–17151
- Roberts WA (2002) Are animals stuck in time? *Psych Bull* 128:473–489
- Roberts WA (2006) The questions of temporal and spatial displacement in animal cognition. In: Wasserman EA, Zentall TR (eds) *Comparative cognition: experimental explorations of animal intelligence*. Oxford University Press, New York, pp 145–63
- Rosati AG, Stevens JR, Hare B, Hauser MD (2007) The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr Biol* 17:1663–1668
- Schwartz BL, Hoffman ML, Evans S (2005) Episodic-like memory in a gorilla: a review and new findings. *Learn Motiv* 36:226–244
- Seligman MEP (1970) On the generality of the laws of learning. *Psych Rev* 77:406–418
- Shettleworth SJ (2007) Planning for breakfast. *Nature* 445:825–826
- Small DM, Zatorre RJ, Dagher A, Evans AC, Jones-Gotman M (2001) Changes in brain activity related to eating chocolate: from pleasure to aversion. *Brain* 124:1720–1733
- Stevens J, Rosati A, Ross K, Hauser M (2005) Will travel for food: spatial discounting in two new world monkeys. *Curr Biol* 15:1855–1860
- Suddendorf T (2006) Foresight and evolution of the human mind. *Science* 312:1006–1007
- Suddendorf T, Busby J (2005) Making decisions with the future in mind. *Learn Motiv* 36:110–125
- Suddendorf T, Corballis MC (1997) Mental time travel and the evolution of the human mind. *Genet Soc Gen Psychol Monogr* 123:133–167
- Suddendorf T, Corballis MC (2007) The evolution of foresight: what is mental time travel and is it unique to humans? *Behav Brain Sci* 30:299–351
- Suddendorf T, Corballis MC (2008). New evidence for animal foresight? *Anim Behav*. doi:10.1016/j.anbehav.2008.01.006
- Szpunar KK, Watson JM, McDermott KB (2007) Neural substrates of envisioning the future. *Proc Natl Acad Sci USA* 104:642–647
- Tangney JP, Baumeister RF, Boone AL (2004) High self-control predicts good adjustment, less pathology, better grades and interpersonal success. *J Pers* 72:271–324
- Tobin H, Logue A (1994) Self-control across species. *J Comp Psychol* 108:126–133
- Tulving E (1972) Episodic and semantic memory. In: Tulving E, Donaldson W (eds) *Organization of memory*. New York Academic Press, New York, pp 381–403
- Tulving E (2005) Episodic memory and autoevidence: uniquely human? In: Terrace H, Metcalfe J (eds) *The missing link in cognition: evolution of self-knowing consciousness*. Oxford University Press, New York, pp 3–56