

Differences in the Cognitive Skills of Bonobos and Chimpanzees

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Abstract

While bonobos and chimpanzees are both genetically and behaviorally very similar, they also differ in significant ways. Bonobos are more cautious and socially tolerant while chimpanzees are more dependent on extractive foraging, which requires tools. The similarities suggest the two species should be cognitively similar while the behavioral differences predict where the two species should differ cognitively. We compared both species on a wide range of cognitive problems testing their understanding of the physical and social world. Bonobos were more skilled at solving tasks related to theory of mind or an understanding of social causality, while chimpanzees were more skilled at tasks requiring the use of tools and an understanding of physical causality. These species differences support the role of ecological and socio-ecological pressures in shaping cognitive skills over relatively short periods of evolutionary time.

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Introduction

Chimpanzees and bonobos are humans' closest living relatives (the common ancestor of all three was around 6 million years ago), and are themselves very closely related (common ancestor around 2 million years ago). Despite their evolutionary closeness, the behavior of these two great ape species differs in important ways, and this might lead us to hypothesize that their cognitive skills differ correspondingly. For example, in their natural habitats, chimpanzees are extractive foragers who use many different types of tools to obtain food from challenging places, whereas bonobos rely on tools very little [1,2]. This might suggest different skills of causal analysis, since using tools effectively requires an understanding of the physical requirements of the situation. On the other hand, bonobos are viewed as being more socially cooperative, and they are temperamentally shyer of new things and more tolerant of others in feeding situations [3,4]. Given recent results with young children in which a clear connection between shy temperament and "theory of mind" skills has been demonstrated [5], we might expect bonobos to have better social-cognitive skills than chimpanzees.

In order to test these hypotheses, in the current study we looked for cognitive similarities and differences in juvenile and adult bonobos and chimpanzees using a broad spectrum of 16 cognitive tasks covering both physical and social cognition. We tested a large number of bonobos and we compared them to similarly aged chimpanzees. The battery of tasks included numerous items assessing a variety of cognitive skills in both the physical and social domains (Primate Cognition Test Battery: PCTB, [6], and see Table 1 and Methods S1; [7]).

The range of cognitive tasks administered has been designed to test the two major evolutionary hypotheses regarding potential

species differences in performance. Given high levels of genetic and ecological similarities [8,9] as well as similar cognitive performance on a range of social and physical tasks (e.g. geometric gaze-following: [10]; gestural communication: [11,12] quantitative discrimination: [13]; liquid conservation: [14] tool properties: [15]; motoric inhibitory control: [16]), phylogenetic inertia predicts few if any significant species differences between the two *Panin* species. In contrast, a socio-ecological model predicts that elements of the battery testing skills related to significant behavioral differences between the two species will reveal species differences in cognitive performance (i.e. even though relative to other apes these two species are highly genetically and ecologically similar). With their more cautious temperament [3,17], social tolerance [4,18,19] and passive coping style [20] bonobos are more likely to outperform chimpanzees in theory of mind tasks, mirroring the positive relationship between shy temperament and theory of mind performance in young children [5]. However, given their greater dependence on a larger range of tools in the wild chimpanzees are likely to outperform bonobos on tasks relating to tool use and causality [2,21].

Methods

Ethics Statement

The presented study was non-invasive and strictly adhered to the legal requirements of the countries in which it was conducted. The study was approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology. Animal husbandry and research complied with the "PASA Primate Veterinary Healthcare Manual" and the policies of Chimpanzee Sanctuary & Wildlife Conservation Trust, Uganda, Tchimpounga

Table 1. Mean performance across scales for females and males of both species and results of species, sex and age differences for the entire sample and matched sample size (bold) and only for entire sample size (non-bold).

Scale	Description	Chimpanzees		Bonobos		Species	Sex	Age
		Female	Male	Female	Male			
Space (4 tasks)	Locating or tracking a reward after location changes.	0.69	0.73	0.71	0.67	ns	ns	positive
Quantities (2 tasks)	Discriminating quantity.	0.67	0.68	0.64	0.66	ns	ns	ns
Tools & Causality (4 tasks)	Causal understanding including tool use.	0.66	0.65	0.57	0.48	Ch>Bo	ns	positive
Social learning (1 task)	Solving a simple but not obvious problem by observing a demonstrated solution.	0.16	0.10	0.13	0.05	ns	m<f	ns
Communication (3 tasks)	Understanding and producing communicative gestures.	0.58	0.56	0.59	0.46	ns	m<f	ns
Theory of mind (2 tasks)	Gaze following and understanding what an actor intended to do.	0.40	0.41	0.51	0.54	Bo>Ch	ns	negative

(Ch = Chimpanzee, Bo = Bonobo, f = female, m = male).

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Chimpanzee Sanctuary, Republic of Congo and Lola ya Bonobo Sanctuary, Democratic Republic of Congo. The vast majority of chimpanzees and bonobos had access to large tracts of tropical forest (5–40 hectares) during the day. In the evening all apes came back from the forest and stayed the night in indoor enclosures (12 m²–160 m²). Apes voluntarily participated in the study and were never food deprived for any reason and they were fed, in addition to the food the apes could eat in the forest, a variety of fruits, vegetables, and other species-appropriate food two to four times daily. Water was either available ad libitum or was given to the subjects several times a day (since most of the apes at the sanctuary spent the day in the forest).

Subjects

We tested 34 bonobos (21 males and 13 females; 5 to 22 years; mean age: 8.5) and 106 chimpanzees (53 males and 53 females; 3 to 21 years of age; mean age: 9.8 and mean age for subsample: 8.5). The bonobos lived at Lola ya Bonobo sanctuary, Democratic Republic of Congo. The chimpanzees lived either at the Ngamba Island chimpanzee sanctuary, Lake Victoria, Uganda, or at the Tchimpounga chimpanzee sanctuary, Republic of Congo. All apes came to the sanctuaries as orphans as a result of the illegal bushmeat trade, were raised by humans together with peers, and at the time of testing the majority lived in social groups.

The chimpanzee data was previously used in Herrmann et al. [6]. Rates of cognitive development differ in bonobos and chimpanzees, and in order to identify the differences in their cognitive skills we did not test infants and used certain methods to control for the effects of age on our sample. Because bonobos and chimpanzees differ in the development of their cognition we did not test infants and used methods to control for the effects of age on our sample in order to identify differences in the cognitive skills of the two species [18].

Procedure

Subjects were tested on the PCTB that comprised 16 different physical and social cognitive tasks (see Table 1, Methods S1 and original study [6]). The tasks dealing with the physical world consisted of problems concerning *space* (4 tasks), *quantities* (2 tasks), and *tools and causality* (4 tasks). The scale space comprised tasks in which the ape had to either locate a reward (spatial memory), track

a reward after invisible displacement (object permanence), after a rotation manipulation (rotation) or after location changes (transposition). The scale quantities was divided into problems in which the ape had to discriminate quantities (relative numbers) or had to discriminate quantities with added quantities (addition numbers). The causality scale included tasks in which the ape had to show a causal understanding either of noise produced by a hidden reward (noise), or a change in appearance produced by the hidden reward (shape) in addition to two tool use tasks. In the first task (tool use) the ape had to use a stick in order to retrieve a reward which was out of reach whereas in the second task the ape had to discriminate between a functional and a nonfunctional tool (tool properties). The tasks related to the social world consisted of problems requiring subjects to imitate another's solution to a problem (*social learning*, 1 task), communicate nonverbally with others (*communication*, 3 tasks), and understand goals and perceptions (*theory of mind*, 2 tasks). The scale communication comprised of one task in which the ape had to understand communicative cues indicating a reward's hidden location (comprehension) and two tasks in which subjects had to produce communicative gestures in order to retrieve a hidden reward (pointing cups and attentional state). The theory of mind scale was divided into a task in which the ape had to follow an experimenter's gaze to a target (gaze following) and a second in which the subject had to understand what an experimenter intended to do (intentions).

No individual had previously participated in a similar study and therefore all individuals were naive to the test situation and tasks. Participants were tested individually by a human experimenter. Each participant completed all tasks in the PCTB within 3 to 5 hours, in the same order across several days of testing. For 11 tasks the subject had to make a choice between two or three potential hiding places. A human experimenter (E) sat behind a table facing the subject through a mesh panel or a Plexiglas window with three holes, through which subjects could insert a finger to indicate their choice. Different setups were used in 5 other tasks. Subjects either had to use a simple tool, solve a simple but not obvious problem by observing a demonstrated solution, gesture to the experimenter or follow the experimenter's gaze direction. The experimenter always waited until the subject was facing her before beginning a trial (more details on each task in

Methods S1). For trials requiring a choice, the position of the reward was counterbalanced across either two or three locations, but the reward was never hidden for more than two consecutive trials in the same place.

Coding and Data analyses

All testing was videotaped. Subjects' responses were initially coded live by E except for gaze-following trials, which E coded from videotape after the test. To be conservative, a reliability coder then independently scored (from videotape) 100% of the trials for chimpanzees. After excellent reliability was established for this species, a second coder then scored the standard 20% of the bonobo trials. The inter-observer agreement for all tasks combined was 99% for both species (for each scale see Table S1).

For the statistical analysis we calculated the proportions of correct responses for each scale. Six separate analyses of covariance (ANCOVA) were carried out, with species and sex as between-subject factors, performance on the six different scales as dependent variables and age as a covariate, to control for the influence of individual differences in age on the cognitive performance.

Results

Table 1 presents comparisons based on the mean percentage of correct trials in each of the six cognitive scales administered as a function of species, sex and age. In support of the behavioral ecological model there were significant differences between species in only two out of six scales – both of which are consistent with observed species differences in behavior. Bonobos scored significantly higher on the “theory of mind” scale ($F_{1,135} = 21.740$, $p < 0.001$) while chimpanzees outperformed bonobos in the tools and causality scale ($F_{1,135} = 23.669$, $p < 0.001$). In this sample of juvenile and adults, age only had a significant influence in the scales where a species difference was found (theory of mind: $F_{1,135} = 7.606$, $p = 0.007$; tools and causality: $F_{1,135} = 12.652$, $p = 0.001$) with older individuals outperforming younger ones in the tools and causality scale (Pearson $r = 0.327$, $p < 0.001$). The opposite was true in the theory of mind scale (Pearson $r = -0.263$, $p = 0.002$). In addition, there was a strong tendency for performance to improve with age in the space scale ($F_{1,135} = 3.849$, $p = 0.052$; Pearson $r = 0.179$, $p = 0.034$). Importantly, age effects did not explain the species differences in performance observed in the theory of mind and tools and causality scales, since no interactions between age and species were detected. Sex differences were also detected in two of the social scales. Females outperformed males in the communication tasks ($F_{1,135} = 6.427$, $p = 0.012$) and showed a strong tendency to outperform them in the social learning scales ($F_{1,135} = 3.593$, $p = 0.06$).

Due to the disparity in sample size between species, and given the potential effect of age on performance, we repeated the analysis after creating an even more conservative sample. Thus, we matched the sample size by selecting chimpanzees that best matched the age and sex composition of the bonobos ($n = 34$ for both species; 72 chimpanzees were dropped from this secondary analysis). This analysis replicates the species differences observed in both the tools and causality scale and the theory of mind scale (theory of mind: $F_{1,63} = 9.962$, $p = 0.002$, bonobos $>$ chimpanzees; tools and causality: $F_{1,63} = 15.891$, $p < 0.001$, chimpanzees $>$ bonobos). In this analysis females again outperformed males in the communication scale ($F_{1,63} = 4.823$, $p = 0.032$) but not in the social learning scale ($F_{1,63} = 1.187$, $p = 0.281$) while previously

detected age differences were no longer significant ($p > 0.064$, in both cases).

Discussion

Overall this broad spectrum comparison of bonobo and chimpanzee cognition demonstrates that species differences in cognition are directly reflected in the most pronounced differences observed in their naturally occurring behavior. Each species outperformed the other on one cognitive scale and in the direction predicted by previous socio-ecological observations, even when controlling for effects of age (i.e. statistically and matching ages). Mirroring individual differences observed in theory of mind development in human children [5], the more cautious and socially tolerant bonobo outperformed chimpanzees on the theory of mind scale. Meanwhile, the prolific tool-using chimpanzee, whose survival is more dependent on extractive foraging, outperformed bonobos in the tool-use and causality scale. This pattern can potentially be interpreted as suggesting that bonobos are more skilled at solving problems requiring an understanding of social causality, while chimpanzees are more skilled at solving problems relating to physical causality. In contrast, the two species did not differ in the scales measuring their understanding of problems related to spatial comprehension, discriminating quantities, using and comprehending communicative signals and learning from others via a social demonstration. This pattern of findings provides support for the hypothesis that socio-ecological pressures play an important role in shaping the cognitive differences observed between these species.

Our sample also allows us to consider differences in performance between sexes in a way that was not possible before. Interestingly, there was little difference between the sexes in their performance across the majority of tasks and the differences were largely inconsistent with previous observations. It is well established that male mammals including humans tend to outperform females on tasks relating to spatial rotation [22] but we did not see the same sex difference here in *Panins*. Moreover, there is little reason to suspect a sex difference between the communicative behavior of male and female *Panins* [12], yet in this study females outperformed males on tasks related to communication. The only sex difference that is consistent with previous behavioral observations is that of females outperforming males in the social learning scale (considering only the entire sample). Long-term observations of wild chimpanzees have suggested that female chimpanzees acquire more proficient tool-using techniques faster than males [23,24] and other studies show a similar pattern in captive bonobos [25]. Therefore, it may be that socio-ecological pressures play a more limited role in producing cognitive differences based on sex in these species, but it also suggests that female *Panins* pay closer attention to others which allows them to learn and solve social problems more quickly and skillfully than males (while both sexes perform similarly in physical cognition tasks).

Finally, while we tried to control the effect of age in our comparisons across species and sex, age is also an important factor to consider in comparing these two species. Wobber et al [18] recently found that bonobos showed delayed development in behaviors and cognitive skills relating to feeding ecology. When we look at the overall effects of age in our analysis we do see that the *Panins* show developmental patterns, but they are somewhat inconsistent (i.e. when the two species are considered together: in some scales they improve in performance with age (space and tools & causality) while in another scale they show decreasing performance (theory of mind)). In general, it has been shown that

inferential abilities in apes increase with age [26] and in particular in the wild older individuals outperform younger individuals in using tools [9,27]. However, a decrease in performance in the theory of mind scale is surprising, but it is not unprecedented (mirror self recognition: [28]; episodic-like memory: [29]).

Overall, this study provides the first experimental comparison of our two closest living relatives in a wide range of cognitive tasks that allow us to examine both species and sex differences in cognitive performance (see [30] for a related primate-wide meta-analysis). While the performance of the two species was mostly similar, the cognitive performance of the two species differed in ways that are consistent with the most pronounced differences observed in their natural behavior. In other words, while the two species are highly similar and only diverged 1–2 million years ago, the observed socio-ecological differences may have shaped each species psychology in predictable ways. The close genetic relationship between chimpanzees and bonobos and the release of the bonobo genome will permit future comparisons between the genomes of the two species which should aid in identifying heritable differences that underlie any such cognitive differences. Understanding how development evolved between bonobos and chimpanzees can then inform hypotheses regarding cognitive evolution in our own species from our last common ancestor with the *Panins*.

Supporting Information

Methods S1 Methods for the Primate Cognition Test Battery.

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Table S1 Inter-observer reliability.

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Author Contributions

Conceived and designed the experiments: EH BH JC MT. Performed the experiments: EH. Analyzed the data: EH. Contributed reagents/materials/analysis tools: EH. Wrote the paper: EH BH JC MT.

Supporting Information for:

Differences in the cognitive skills of bonobos and chimpanzees

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Methods for the Primate Cognition Test Battery (taken from supplementary online material in Herrmann et al. 2007)

Materials and Apparatus

A wooden table (80 cm × 39 cm) with a sliding platform (78 cm × 35 cm) was used for the experiment. Three blue (Ø 10 cm × 8.3 cm height) or other materials (which are reported in Procedures section) were used to cover / present the food reward; these were placed on the sliding platform 58 cm apart (in case of three cups ~20 cm apart). The testing table on which the sliding platform was attached was either placed in front of a Plexiglas testing window (69 cm × 48 cm) with three hand holes (6 cm in diameter) or a mesh panel (opening in the mesh 5 cm²). Subjects could reach their fingers through the holes or the mesh wire to make a choice. Throughout testing, unless otherwise indicated, a choice was scored as the first cup that a subject indicated with their finger. Different cups and containers were used as hiding places. When the apes indicated the correct location they were given a small food reward. However, unless otherwise stated, when the apes made incorrect responses they were always shown the location of the hidden food after each trial. The same desirable food items were used as rewards for most of the tasks. For chimpanzees, this consisted mainly of banana pieces, whereas apple pieces served as rewards for bonobos. However, depending on the subjects' motivation and some of the demands of the different tasks, different food rewards were used (i.e. for the quantity tasks, either raisins or peanuts were used as countable food items).

Procedures

Physical Domain

1. Space

a. Spatial Memory

The experimenter (E1) showed the subject two rewards and then placed the rewards under two of the three cups, which stood in a row on the platform while the subject was watching. E1 then pushed the platform forward and the subject was allowed to make up to two choices in succession. However, if subjects chose the empty container, no further choices were possible. To count as a correct response subjects had to choose both baited cups in succession.

b. Object Permanence

The experimenter (E1) placed three empty cups in a row on the platform. Then E1 placed an additional small opaque cup on the far left side of the platform and placed a reward under it in full view of the subject. After the reward was placed under the small cup, one of three possible displacements was conducted:

Single displacement: The experimenter moved the small cup containing the reward under one of the three cups, leaving the reward under this cup without touching the other two cups.

Double adjacent displacement: The experimenter moved the small cup containing the reward under two adjacent cups in succession, leaving the reward under one of these cups without touching the third cup.

Double non-adjacent displacement: The experimenter moved the small cup containing the reward under the left and right cups while skipping the center cup (i.e. not touching it). As before, the reward was left under one of the two manipulated cups.

After hiding the food piece under one of the cups, E1 showed the subject that the small cup, used to bait the other cups, was empty. Then the subject was allowed to make either one choice (in the single displacement item) or up to two choices (in the double displacement items). If the subject chose a cup that had not been manipulated during the demonstration, no further choices were possible. To count as a correct response subjects had to choose the baited cup before choosing a cup which was not manipulated at all.

c. Rotation

Three cups were aligned in a row on a tray placed on the testing platform. E1 then showed a reward to the subject and placed it (in view of the subject) under one of the three cups. Then the tray was spatially manipulated in one of three ways and the subject was allowed to choose one cup in order to correctly locate the food:

180° middle: The reward was placed under the middle cup, and the tray was rotated 180° in clockwise direction. Thus, the reward was ultimately in the same location that it was originally placed.

360°: The reward was placed under either the left or right cup, and the tray was rotated 360° in clockwise direction. After the rotation, the reward was in the same location as it was originally placed.

180° side: The reward was placed under either the left or right cup, and the tray was rotated 180° in clockwise direction. Therefore the reward was ultimately located on the opposite side of where it was originally placed.

To count as a correct response subjects had to choose the baited cup first.

d. Transposition

Three cups were placed in a row on the testing platform. E1 then showed a reward to the subject and placed it (in view of the subject) in one of the three cups. Then one of three manipulations of the baited cup was conducted and the subject was allowed to choose one cup:

Single transposition: E1 switched the position of the baited cup with one of the empty cups without touching the third cup.

Double unbaited transposition: E1 first switched the baited cup with one of the empty cups, and then switched the positions of the two empty cups.

Double baited transposition: E1 switched the baited cup with one of the empty cups, and then switched the baited cup again with one of the empty cups.

To count as a correct response subjects had to choose the baited cup first.

2. Quantities

a. Relative Numbers

E1 placed two dishes on the testing platform, then hid them from the subjects' view with an occluder. E1 then baited them with different amounts of equal sized food pieces (half a peanut or raisin was used as a unit). E1 then covered the dishes with lids and placed them in the middle on the platform. The occluder was then removed, after which E1 lifted the lids of both dishes simultaneously so that subjects could see the amounts in each. After ~5 seconds had passed, E1 moved the open dishes to the sides of the platform, one on the right and one on the left, and the subject was allowed to

choose one. Each subject received one trial for each of the following pairs of numbers that were always presented in the same order for all subjects: 1:0, 5:1, 6:3, 6:2, 6:4, 4:3, 3:2, 2:1, 4:1, 4:2, 5:2, 3:1 and 5:3.

To count as a correct response subjects had to choose the larger quantity first.

b. Addition Numbers

E1 baited three dishes with different amounts of reward (same as in Relative Numbers) behind an occluder, covered them with lids, and placed them in the middle of the platform. The occluder was removed, and E1 then lifted the lids of the two side dishes simultaneously. After ~5 seconds, E1 covered the side dishes and uncovered the one in the middle. Subjects could view the contents of the center dish for ~5 seconds, and then E1 transferred the rewards from the center dish to one of the side dishes. During the transfer the subject could not see the content of the side dishes. Then E1 removed the empty center dish and the subject was allowed to choose between the two closed side dishes. Each subject received one trial for each of the following pairs in the same order: $1:0 + 3:0 = 4:0$; $6:1 + 0:2 = 6:3$, $2:1 + 2:0 = 4:1$, $4:3 + 2:0 = 6:3$, $4:0 + 0:1 = 4:1$, $2:1 + 0:2 = 2:3$, $4:3 + 0:2 = 4:5$.

To count as a correct response subjects had to choose the larger quantity first.

3. Causality

a. Noise

The experimenter (E1) hid a reward in one of two opaque cups; during baiting the cups were behind an occluder so that the subjects could not see in which cup the reward was hidden. After removing the occluder, E1 manipulated the cups in one of two ways:

Noise full: The experimenter shook the baited cup three times so that the food rattled inside and then simply lifted the empty one without shaking it.

Noise empty: The experimenter shook the empty cup (producing no sound) three times and then lifted the baited one without shaking it.

To count as a correct response subjects had to choose the baited cup first.

b. Shape

E1 hid a reward underneath one of two identical pieces of plastic or cloth, which were placed on the platform. During baiting the pieces of material were behind an occluder, so the subject could not see the experimenter placing the reward. Once the occluder was removed, the subjects were confronted with one of two situations and were allowed to touch one piece of material to locate the hidden food:

Board: The reward was hidden underneath one of two plastic boards (20 x 15 cm). The food's location was visually apparent since the baited board was inclined as it was placed on the food (the other board remained flat on the table).

Cloth: The food was hidden underneath one of two pieces of cloth (20 x 15 cm). The reward made a visible bump under this piece of cloth (the other cloth remained flat on the table).

To count as a correct response subjects had to choose the baited board or cloth first.

d. Tool Properties

E1 placed two different tools and an equal sized reward for each tool on the

platform behind an opaque screen. One tool was functional and could be used to retrieve the reward associated with it, whereas the second tool was non-functional and could not be used to obtain the associated reward. Each subject participated in five different items:

Side: The potential tools consisted of two identical pieces of cloth (20 cm x 15 cm). A reward was placed on top of one cloth piece, whereas the other reward was placed directly next to the other cloth piece (i.e. making the second tool ineffective for retrieving the food). Thus, the subject could only retrieve a reward by pulling the piece of cloth with the reward on top of it.

Bridge: A Plexiglas bridge was placed over each of the far ends of the two identical cloth pieces. For one of the potential cloth tools, the reward was placed on top of the bridge (making the tool ineffective in retrieving the food). On the other side, the reward was placed on the cloth underneath the bridge. Thus, the subject could only obtain a reward by pulling the cloth with the reward placed directly on it.

Ripped: A rectangular, intact cloth piece (20 cm x 15 cm) was positioned on one side of the table, and two smaller cloth pieces (11 cm x 15 cm and 8 cm x 15 cm) were positioned on the other side. The two small pieces of cloth were placed on the table such that there was a 1 cm gap between them, which visually emphasized that they were disconnected. Importantly, when combined, the two small pieces of cloth – including the 1 cm gap between them – were of identical length and width as the one functional large piece. Once the cloths were in place, a reward was placed on top of the far end of the intact cloth, and the other was placed on the out of reach piece of the two disconnected pieces (making them ineffective as tools). The subject could only acquire a reward by pulling the large, intact cloth piece.

Broken wool: This item was identical to the Ripped cloth item with the exception that pieces of wool string were used instead of cloth: one piece of wool was intact, whereas the other was cut in two pieces. The reward was tied to the far end of the wool pieces out of the subject's reach, so a reward could only be acquired by pulling the intact piece of wool.

Tray circle: Two small plastic trays (15 cm x 4.5 cm) were placed on the platform. One tray had a hole cut out of it that formed a circle (3.5 cm in diameter) around a reward placed inside. The other tray had a u-shaped hole cut out of the back of it so that if a reward was placed "in" it the tray surrounded the food but did not hold it. A string was then attached to both trays that could be used to pull the tray and the reward within reach. Subjects could obtain the reward if they pulled the rope which was attached to the tray with the circle-shaped hole, as the material at the back of the tray pushed the reward forward.

A correct response was scored if the subject first chose the functional tool by pulling it.

Social Domain

1. Social Learning

For each of the following social learning tasks the subject was given two minutes to solve the problem after E1 demonstrated the solution. For all three tasks we established a baseline with twelve chimpanzees during the pilot phase at the Wolfgang Köhler Primate Research Center in Leipzig, Germany. Without demonstration none of the twelve subjects solved the problem with the same means we demonstrated in the following three tasks (i.e. making it likely that any reproduction of the demonstrations described below are due to social influences).

A correct response was scored only if the subject not only obtained the reward but did so by using a means highly similar to that they had seen previously demonstrated.

a. Paper Tube

A reward was placed inside a 20 cm long transparent plastic tube with a piece of paper attached over both ends. E1 demonstrated for the subject how to open the tube: First E1 poked her finger through the paper on one end and then wiggled her finger in the tube to rip the paper further, making the hole in the paper larger (i.e. as opposed to using her mouth or hands to tear the paper off the tube). Finally, E1 tilted the tube in order to let the reward fall in her hand. After the demonstration E1 handed an identical tube to the subject.

b. Banana

A small slice of banana was placed in the center of a 30 cm long transparent Plexiglas tube. The reward was trapped in the tube, such that a specific force had to be applied to get the reward out of the tube. E1 demonstrated for the subject how to get the reward out by banging one end of the Plexiglas tube on the floor (as opposed to shaking it forcefully). After the successful demonstration, E1 handed an identical tube with a banana inside to the subject.

c. Stick Tube

An opaque plastic tube with caps on each end was baited with a reward. One of the caps had a hole in it but was glued to the tube, whereas the other cap had no hole but could be removed. E1 demonstrated for the subject how to open the tube: First E1 inserted a stick through the cap with a hole, and then she pushed the stick through the hole which forced the cap on the other end to fall off. After the successful demonstration E1 handed an identical grey tube to the subject.

2. Communication

a. Comprehension

The experimenter (E1) hid a reward under one of two cups that were placed in a row on the testing platform behind an occluder. After removing the occluder, E1 gave one of three social cues before giving the subject the opportunity to search in one of the cups.

Look: E1 sat in front of the cup and alternated her gaze between the subject and the baited cup three times while calling the subject's name. After the first three gaze alternations E1 continuously looked towards the cup until the subject chose.

Point: E1 sat in front of the cups and continuously pointed to the baited cup with the extended index finger of her cross-lateral hand. At the beginning of the point, she alternated her gaze between the subject and the cup three times while calling the subject's name and then only stared in the baited cup's direction.

Marker: E1 placed an iconic photo marker, which depicted the reward, on top of the baited cup. Before the placement, E1 held the photo in her hand and alternated her gaze three times between the photo and the subject while calling the subject's name.

To count as a correct response subjects had to choose the baited cup first.

b. Production: Point Cups

In the following task, E1 indicates the person who was the main experimenter throughout testing, whereas E2 indicates a second helper. Two cups served as hiding places. These cups were placed on two separate tables. The hiding places were spread

120 cm apart and both equidistant from the subjects' starting point between the two hiding places. E2 entered the testing area, placed a reward under one of the two cups in full view of the subject, and then left the area. Then E1 entered the testing area and centered the ape by giving her a piece of food between the two tables. Then E1 stood equidistant to both cups and waited until the subject approached one cup and indicated it. If the subject indicated first the correct cup within one minute, E1 gave the reward to the subject and a correct response was scored.

c. Production: Attentional State

In the following task E1 indicates the person who was the main experimenter throughout testing, whereas E2 indicates a second helper. Subjects participated in four different items in which the attentional state of E1 varied. In all items the trial started when E2 entered the testing area and placed a reward out of reach but in front of the subject's room – either on its right or left side. Then E2 left the area. Next E1 entered the testing area, but stood on the end of the room opposite of the reward and thus did not notice the reward on the floor. Then E1 stood and looked in four different ways:

Away: E1 turned around and looked away from the reward. The subject had to approach E1 from her front in order to see each other. If the subject approached E1 within 20 seconds (20s), E1 turned around and waited for the subject to direct her attention to the reward. If the subject went back to the reward's location and indicated the reward within 20s, E1 handed the reward to the subject.

Towards: E1 looked towards the reward. E1 waited for the subject to approach the reward and to direct her attention towards the reward within 20s. If the subject indicated the reward within 20s, E1 handed it over to the subject.

Away Body-facing: Identical to Away, except that E1's body faced toward the reward and only the face was turned away.

Towards Body-away: Identical to Towards, except that E1's body was turned away and only the face was directed towards the reward.

The subjects could indicate the location of the hidden food by pointing to the location of where the reward was hidden if the location was in view of E1 or by first moving into E1's view (i.e. trying to obtain her attention) and then pointing to the correct location when E1 initially could not see the reward location. In all of the items, if the subject never approached or overtly indicated to E1 the location of the food, E1 left the testing area and E2 came back to remove the reward.

3. Theory of Mind

a. Gaze Following

E1 sat in front of the subject and gave a piece of food to the subject in order to attract her attention. Once the subject sat and looked at the experimenter, E1 started the trial. Each individual received three different items (which were conducted on a different day within the test battery to minimize any kind of habituation):

Head + Eyes: E1 called the subject's name and showed them a piece of food before hiding it in her hand, which remained in front of her body. Then E1 looked up with both her head and eyes (eyes open) for ~10s.

Back: E1 sat with her back facing the subject. E1 called the subject's name and showed them a piece of food before hiding it in her hand, which remained next to her shoulder. Then E1 looked up to the ceiling for ~10s. Within the ~10s E1 looked back over her shoulder at the subject three times to ensure that the subject was still paying

attention. If the subject was not paying attention when E1 looked the second time, the trial was repeated.

Eyes: E1 called the subject's name and showed them a piece of food before hiding it in her hand, which remained in front of her body. E1 glanced up at the ceiling for ~10s while her face was still facing the subject.

A correct response was obtained if the subject followed the gaze of the experimenter.

b. Intentions

E1 hid a reward in one of two cups placed in a row on the platform behind an occluder. After removing the occluder, E2 manipulated the cups in one of two ways:

Trying: E2 tried unsuccessfully to open the baited cup by removing the lid while looking at the cup.

Reaching: A mesh or Plexiglas barrier blocked E2's access to the cups. E2 unsuccessfully tried to reach the baited cup by extending the equilateral arm, looking at the correct cup. She continued to give this cue until the subject indicated a choice.

For both items, ~3s after each demonstration E1 approached the table and pushed the platform forward so that the subject was allowed to make a choice. To count as a correct response subjects had to choose the baited cup first.