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Individual Differences in Long-term Cognitive Testing in a Group of Captive Chimpanzees

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Seven chimpanzees had participated in cognitive tasks from the time they were approximately 18 months to approximately 16 years of age when the data presented here was analyzed. Testing covered a wide range of tasks, which we categorized broadly as measuring their understanding of aspects of either their social or physical environments. Therefore, we could test whether individuals who excelled on 'social' tasks, also excelled on 'physical' tests. We also categorized our measures as ones of acquisition, criterion, retention or transfer of skill. Thus, we could determine whether individuals who mastered tasks quickly were also those who performed, remembered and generalized tasks most accurately. We were interested in whether there were consistent patterns in cognitive skills across tasks and measures. Results of our analyses indicate that, as with humans, chimpanzees vary in their performance across some measures, although some differences in cognitive skill between individuals are also consistent across measures and tasks. The results have implications for questions concerning domain generality or specificity of cognitive skills in another primate species.

Pioneers in the history of psychology from the polarizing influence of Galton (1961) and his cousin Charles Darwin (Darwin, Richards, Galton & Diamond, 1997) to followers like Cattell (1941) promoted the study of individual differences. Although the focus on individual differences has largely given way to the normative approach of G. Stanley Hall and Gesell (Anandalakshmy & Grinder, 1970; Borstelmann, 1974), those who study human cognition continue to value the importance of attending to individual variance (Embretson & Prenovost, 2000; McMurray, Samelson, Lee, & Tomblin, 2010). Those who make use of human participants in research have the luxury of access to large numbers of participants, where outliers tend to have less of an influence on statistical results and, with large enough sample sizes, randomization takes care of most extraneous variables. However, for those working with small N groups, such as the majority of comparative researchers, the statistical influence of individual variance is perhaps more significant, and the impact on our conclusions more profound, yet this issue has been largely neglected in the literature, despite the groundbreaking work of Tryon as far back as 1930.

Comparative researchers often rely on data from few subjects, or even a single subject, as an ambassador for an entire species, or taxonomic group. Data from Alex the African Grey parrot on categorization, language, numerosity and

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abstract representation represents that for the parrot family as a whole (Pepperberg, 2006). Similarly, work with a single New Caledonian Crow, Betty, sparked an interest in corvids as tool-users (Weir, Chappell, & Kacelnik, 2002; Weir & Kacelnik, 2006). Research groups working with other members of the same species have had difficulty replicating the most sensationalized results of Alex and Betty in other members of the species (Holzhaider, Hunt, Campbell, & Gray, 2008; Pepperberg, 2002a, b; Pepperberg, Gardiner, & Luttrell, 1999; Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009). Sue Savage-Rumbaugh's work with Kanzi alone has led many to speculate that bonobos are superior to chimpanzees in their ability to acquire and manipulate symbols that represent a 'human-like language' (Savage-Rumbaugh et al., 1993). This 'holy grail' approach is arguably less problematic (from the small N perspective) as the goal of the research is to demonstrate that a species is capable of mastering a particular skill, and then it is minimally necessary to show that only a single member is able to master the task – not that all members can acquire it. This conclusion of course rests on the assumption that the task itself is a valid indicator of the underlying cognitive process, which is difficult to accomplish in any one test, or even series of tests. These problems are compounded when the tests are administered to a single research subject raised in a unitary environment, which may not be very representative of what the species would experience naturally.

Thus, if the goal of the research is to understand the average capacity of the species or the range of abilities, or to compare the natural abilities of the species in wild versus captive environments and to fully comprehend how the abilities emerge, reasonably large samples are required. Having a nonrepresentative sample may influence the conclusions a researcher draws in a profound way. In addition, if you have an 'exceptional' research subject who is motivated and skilled at the tasks you present in the lab, then you will conclude that the species holds that capacity. But what if you happen to have four or five parrots, bonobos, chimpanzees or crows at your disposal, none of which are motivated or interested in the tasks you present? Would it be accurate to conclude that that species is incapable of comprehending the tasks those particular members have not demonstrated evidence of understanding simply because they haven't performed the tasks to your human determined criteria? Non-humans may or may not perform the tasks we present for a variety of reasons – some having to do with their understanding of the task, and some due to other factors – motivational or situational – such as a long history of experimental training which could contaminate any further study. Individual differences are thus a huge factor in the conclusions we draw regarding the abilities of a species, and they may be faulty conclusions. While most of us would not want the cognitive abilities of the entire human race to be represented by a developmentally delayed adult with an IQ of 80, it would be no more accurate to have those abilities represented by Albert Einstein or Thomas Edison, as the latter's brief foray into designing intelligence tests for the masses proved (Dennis, 2006).

Thus, it is critical to ascertain how much variance exists in the cognitive abilities of members of other species. One question is whether there is considerable variation in cognitive ability in non-human species and whether this variability itself varies as a function of cognitive complexity. One might suppose that other

primates, particularly the great apes, might be more likely to show individual differences in cognitive skill, whereas single-celled organisms, and maybe even the white rat, may show less variability. However, even the laboratory rat can show variability in its ability to learn a maze, as different strains have been bred and selected for on the basis of that very trait (Tryon, 1930). Keagy, Savard, and Borgia (2009) showed that male problem solving ability predicted mating success in bowerbirds indicating that such variability can predict reproductive fitness.

A second question is whether we can measure cognitive ‘skill’ or intelligence as a domain general ability. That is, if it varies within individuals, does it generalize across tasks such that an individual who is intellectually superior is so across different measures of ability? Are the individuals we have identified as “bright” in the lab equally skilled at many tasks or only particular subsets of tasks – and can we identify particular types of subsets that certain individuals can perform well but not others, just as we can with humans? In the laboratory rat, it has been demonstrated that maze brightness doesn’t always transfer to superior performance on other cognitive tests (Loevinger, 1938). Here we define “general intelligence” as the ability to rapidly acquire and apply information to successfully solve problems when presented in novel contexts, across a variety of domains. Surprisingly little rigorous work has been conducted with any non-human species, although recent work with mice suggests that variation in some components of the working memory system – or its animal analog – co-vary with measures of general intelligence (Matzel & Kolata, 2010). This work suggests that selective attention and working memory are key factors in the variability of general intelligence in a wide variety of animal species. Thus, the data so far from rats alone is mixed.

A related question is whether non-humans who master tasks tapping into one particular cognitive domain are likely to be equally skilled in tasks tapping into a different domain. Years of testing with human participants both within and outside of the educational system have suggested to us that humans might excel in particular domains, but not others. For instance, some individuals can be skilled in math and science but not in languages and the arts and vice versa (Brunner, 2008). Others are what we deem to be more “well-rounded.” However, surprisingly little empirical work has directly tested such propositions. Work by Wellman, Lopez-Duran, LaBount, and Hamilton (2008) at least suggests a special social intelligence, in that infants who are skilled at social tasks later perform well on theory of mind tests, even when more generalized measures of cognitive ability, such as IQ and executive function are controlled for. However, we do not know if there is an equivalent skill set for solving problems of a physical nature, or how infants who are socially skilled would perform on such tasks. Correspondingly, we do not know if non-humans should perform equally on, for instance, tests of social versus physical causality. There is only very preliminary work on these questions in only a few species. Brauer, Kaminski, Riedel, Call, and Tomasello (2006) presented several dogs and apes (chimpanzees and bonobos) with a variety of cues that were designated as either social or physical in nature, and were intended to inform the subjects as to the location of hidden food. Consistent with the authors’ predictions, the dogs were best able to find the food when directed with social cues such as pointing, while the apes were best able to find the food when informed with physical cues such as the sound of the food being shaken in baited cups,

versus silent unbaited cups. This is a welcome empirical attempt to tease apart social and physical reasoning processes in several closely and distantly related species; however it is more limited in scope compared to the recent project as it deals only with the object choice paradigm – a paradigm that has been heavily criticized in terms of what it can and can not inform us about an animal's reasoning (Heyes, 1998; Penn & Povinelli, 2007; Povinelli & Vonk, 2003, 2004).

Despite these limitations, some theorists have made much of such species differences, speculating that domestic dogs evolved such abilities through the process of domestication (Hare, Williamson, & Tomasello, 2002; Kubinyi, Virányi, & Miklósi, 2007), ontogenesis (Dorey, Udell, & Wynne, 2010; Udell, Dorey, & Wynne, 2008; Wynne, Udell, & Lord, 2008) or because of their natural social structure, which highlights cooperation among members of the pack (Mech & Boitani, 2003). One of the reasons we might be interested in such divergence pertains back to the issue of variability. Rather than assuming less variability in cognitive skill overall in other species, we might assume their abilities to be less variable in certain domains than in others. So for instance, if solving problems in the physical domain are tantamount to survival but a species need not reason about complex social interactions, one might expect less variability among individual members of that species in their social reasoning, compared to their physical reasoning. The opposite might be true of species like chimpanzees, canines, and corvids who live in large social groups.

Comparing performance on social versus physical tasks is theoretically interesting for a number of reasons. Cosmides (1989) suggested that humans are biologically prepared to reason socially in particular contexts, but it is largely unknown whether non-humans show the same predisposition, and given that it is still contentious whether non-humans share any elements of the theory of mind system (Call & Tomasello, 2008; Emery & Clayton, 2007; Focquaert, Braeckman, & Platek, 2008; Penn & Povinelli, 2007; Povinelli & Vonk, 2003, 2004; Tomasello, Call, & Hare, 2003a, b), it seems plausible that they may show the opposite predilection. That is non-humans may be especially prepared to reason in nonsocial contexts. Indeed, to our knowledge no empirical work has investigated whether potential differences between social and physical reasoning processes vary between individual humans, or even between typically developing humans and those with developmental disorders such as autism, despite a growing body of literature, suggesting that they might (Zaitchik, 1990). Current tests are underway to investigate the hypothesis that typically-developing human children show advantages for solving analogies when the stimuli are social versus non-social in nature (Beckman, Biondillo, & Vonk, in preparation).

Recently, Herrmann, Call, Hernandez-Lloreda, Hare, and Tomasello, (2007) conducted a large scale project to compare the social and physical reasoning skills of human children, chimpanzees and orangutans. These authors concluded that children and chimpanzees had similar skills for dealing with the physical world, both showing superior skills to those of orangutans, but that children were more adept at solving social problems, relative to both ape species. Although see Lyn, Russell, and Hopkins (2010), who conducted some of the same tests with enculturated and non-enculturated chimpanzees and bonobos, and suggested that the differences between apes and children on social tasks were due

to differences in rearing environments rather than species differences. Lyn et al.'s work (2010) points to the importance of considering individual differences in rearing history when drawing conclusions about species differences in cognitive ability and evolved traits. Herrmann et al. (2007) found no evidence for species differences in individual cognitive variability. Based on the results of this battery of fifteen cognitive tasks, Herrmann, Hernández-Lloreda, Call, Hare, and Tomasello (2010) later ran additional analyses to determine whether individual differences in performance for the chimpanzees and the children could be best explained by a single factor, general intelligence – *g*, a two factor model, which included components for social and physical intelligence, or a three factor model, which included components for spatial, physical and social intelligence. They found that the three factor model best fit the data for children, suggesting multiple intelligences, but that the data for the chimpanzees was best fit by a two factor model – one that included a factor for spatial intelligence but another factor that combined physical and social intelligence together. Their analyses revealed no evidence for individual differences in social and physical reasoning skills. In a larger meta-analysis of many studies of various non-human primates, Deaner, van Shaik, and Johnson (2006; see also Lee, 2007) found support for the idea that primate evolution has favored a general intelligence, which allows different species to excel at several different types of tasks across domains, relative to members of other genera, but it is important to note that this study did not include social tasks.

A related question, and one not tested by Herrmann et al. (2010) with regards to domain general versus specific cognition in non-humans, is whether different measures of ability tap into general cognitive ability, or specific skill sets? Are those subjects who master tasks the most quickly the ones who ultimately perform the most accurately, and who also generalize at the highest levels on tests of transfer performance? Thus, is there consistency between acquisition and mastery of a cognitive skill? Conceivably, acquiring mastery and grasping how that skill maps on to novel situations and objects are two very different cognitive abilities and may not be superior in the same individuals. However, if there is a general intelligence that allows non-humans to excel in cognitive tests in the lab, one might expect the same individuals who learn tasks quickly will also attain the highest levels of performance, have the highest scores on first trial measures of novel tests and tests of transfer and also retain that performance when given retention measures on previously learned tasks. However, if intelligence or cognitive skills are less domain-general and more specialized we should see more variation in performance of these different measures. Therefore, in addition to classifying the broad nature of cognitive domain, we also separately categorized our tasks as measuring acquisition, mastery, retention and generalization of skill. Such analyses should help to ascertain to what extent cognitive skill is generalizable and across what types of lab-based tasks. Such analyses had not previously been conducted on such a large scale with great apes until the recent analysis published by Herrmann et al. (2010). Whereas the Herrmann et al. study tested a large number of both chimpanzees (106) and human children (105), they tested both species on 15 tasks. We tested our seven chimpanzees on a larger number of tasks (approximately 136 total tasks) over more

than a decade. Additionally, we will focus more on differences between the individual participants on different measures of their performance in our analyses.

The current project is a preliminary attempt to investigate whether individuals differ in the extent to which they perform tasks designed to tap into social versus physical reasoning processes, and whether differences between individuals are consistent across tasks and different measures of performance. To accomplish this, we mined the data archives of the Cognitive Evolution Group, which has investigated a group of seven chimpanzees who have engaged in cognitive testing from the time they were 18 months of age until they were about 16 years of age, to collect the information for this study. One obvious difficulty is that classifying a large number of tasks into broad categories loses some of the nuances of the tasks. So a caveat of the current project is that the designations of type of task, for example, have to be, by definition, a bit coarse.

Method

Participants

The data for all analyses were derived from the archival experimental records of the testing of seven chimpanzees (one male, Apollo (APO) and six females, Mindy (MIN), Jadine (JAD), Kara (KAR), Brandy (BRA), Candy (CAN), and Megan (MEG)). These chimpanzees were housed in a single social group at the University of Louisiana's Cognitive Evolution Group (for a history of the group, see Povinelli, 2000). They had begun training and familiarization with an animal trainer from the time they were 18 months of age and had participated in daily cognitive and behavioral tests since they were 2-3 years of age. The chimpanzees ranged in age from 15.6 to 16.5 years of age at the time that this meta-analysis was conducted.

Materials

Materials varied widely depending on the study from which the data was taken. Most of the social tasks involved the participants interacting with human experimenters, from whom they begged using a species typical begging gesture, through holes cut into a Lexan barrier that divided an indoor test enclosure into participant and human experimenter areas. Experimenters may have covered their faces with buckets, blindfolds or other objects in some of the studies. Other studies involved objects such as boxes, and surprising objects such as stuffed animals. Physical tasks often involved tools (see Povinelli, 2000), weighted objects, wooden trays, apparatuses such as ramps, boxes containing pivoting shelves and other devices to test their understanding of the physical world.

Procedure

The first author conducted a meta-analysis of results from the archives of the second author's laboratory, where data from all phases of all experiments are recorded both on original data sheets and on DVD or videotape. Experimental protocols, amendments and deviations signed by all principal investigators and study directors, as well as the animal trainers involved in the study document the details of each experiment. From this information it was possible to determine how each task presented to the chimpanzees should be classified. If it was not possible to determine the classification of the task because the study description was not sufficiently detailed, or data was not recorded for all subjects, the experiment was not included in the analysis. Furthermore, if the study could not be clearly classified as measuring either social or physical understanding, the study was excluded from the analysis. All of the original testing data had been subjected to reliability where an independent rater had coded the data on the data sheets from videotape to a Cohen's Kappa (κ) of 0.70 agreement or greater (typically $\kappa > 0.90$). Some of the training data had not been subjected to inter-rater reliability.

Task Classification

Social versus Physical. In terms of nature of task or cognitive abilities tapped into by our tasks (general domain), we chose to classify our tasks as social versus physical, where social tasks were defined as those that measured our chimpanzees' abilities to discern the social behavior /mental states of other individuals. For instance the social tasks included studies in which the chimpanzees engaged in joint visual attention to follow the gaze or line of sight of human experimenters, determined which of two human experimenters to beg from using a visual begging gesture, and followed human pointing cues to find hidden food. Not all participants contributed data to the same number of tasks as not all completed all phases of training or entered the testing phase of all studies that were analyzed for the current project. On average, approximately 18 training tasks, and 25 tests were designated as social for each participant. Physical tasks were defined as those that measured our chimpanzees' abilities to use tools or determine the physical cause of an event they were to reason about, such as weight, rigidity, contact, etc. For example, these studies included those in which chimpanzees had to decide which tool to use to procure rewards from an apparatus, or which way to orient a tool to insert into an apparatus, or to reason about the properties of an object and how those properties would impact on other objects or the environment. On average, about 45 training studies and 48 tests were classified as physical tasks for the purpose of these analyses for each participant. The appendix provides a list of experiments and their classification for each subject.

Training tasks and tests belonged to the same study. Training tests were conducted in order to introduce the participants to the study objects and the basic physical manipulations required for the task. For instance, if the study required the animal to make a discrimination between two individuals who might offer a food reward, and the critical discrimination in testing was that only one individual could see the begging gesture, the training task would simply require the chimpanzees to meet a criterion for entering the testing unit and making a begging response consistently to a single individual. This might be a training regime for a social test. If the task would ultimately require the chimpanzee to choose between two tools, only one of which could be used to procure food reward, because of its functional properties, the training task might allow the chimpanzees to use the tools individually outside of the critical testing context to become familiar with their properties. This would be an example of training for a physical test.

Acquisition, Mastery, Retention. In order to determine whether different measures of performance tapped into different skill sets, the tasks (both social and physical) were separately classified as measuring acquisition, mastery and retention. If the chimpanzees were being trained to perform a task they had never performed before, that was not part of their natural behavioral repertoire, the number of trials taken to reach criterion was used as a measure of acquisition for a novel task. First trial performance (that is, percentage of trials correct on the first session performing a new task) was taken as an indication of mastery. If participants were being re-trained to criterion on a task they had already learned, the number of trials to reach that criterion performance level again was considered a measure of retention.

Novel, Familiar, Transfer. We also classified our tasks as measuring novel skills; ability to perform familiar tasks, and generalize previously learned skills to novel objects or contexts. If the task was a first test of some skill or combination of acts the participant had not performed before, or with some object the participant had not encountered before, it was considered a novel task, but if the task was transfer to a novel object or context within the same skill set, it was considered a generalization or transfer test. If the same task with familiar objects was presented again at a later time point, it was considered a retention task.

Given the lack of prior data bearing on this topic it is difficult to make firm predictions but there are a number of testable hypotheses. If there are certain domains or modules for social reasoning, in the primate brain, one might expect that some chimpanzees perform better on social tasks than physical tasks. However, if being socially skilled is considered an evolutionary adaptation, thus explaining why evolution gave rise to social cognition in the ape lineage to begin with, one might expect that those who excel at social tasks also excel at all tasks generally and thus might also excel at the physical tasks. Thus, individuals who perform well on social tasks should perform well on physical tasks, and should also acquire tasks more quickly and outperform other individuals on measures of trial one performance and transfer. Of course, it is not necessary to assume that reasoning in the two domains is mutually exclusive, or that evolution has selected for reasoning in only one domain. Chimpanzees could be expected to have sophisticated skills in both domains with

many individuals excelling at both social and physical tasks, not because of some domain-general ability, but because there are particular modules for both social and physical reasoning. A factor analytic approach would be better suited for differentiating between models of general intelligence and modular models of cognition than the approach we have taken here. However, if there are differences in performance between social and physical tasks, this is a preliminary step to indicating differences in reasoning within these domains within a small sample size. If this is the case, there should be some variance, even within our small sample, on how apes perform on these various tasks and measures as it is assumed that there are individual differences in cognitive performance in chimpanzees, in both domains and measures of skill.

Results

Task Measures

The first question we asked was whether there was a statistical relationship between the number of trials required to reach criterion (task acquisition) and first trial accuracy (mastery) collapsed across trials of all types (social and physical, novel, retention). The data from the present study comprised a multilevel data structure because observations at one level of analysis (i.e., task) were nested within another level of analysis (i.e., participants). Due to the hierarchical structure of the data, a multilevel random coefficient model (MRCMs) using the program HLM (Bryk, Raudenbush, & Congdon, 1996) was conducted on the average number of trials to reach criterion on all training tasks against the average percentage of trials correct on the first session of testing once criterion had been obtained on the training for the task for each participant. There was a significant negative relationship such that participants who reached criterion in fewer sessions achieved higher scores on the first session of testing, $B = -0.44$, $t = -7.11$, $p < 0.001$. This result suggests a relationship between task acquisition and mastery.

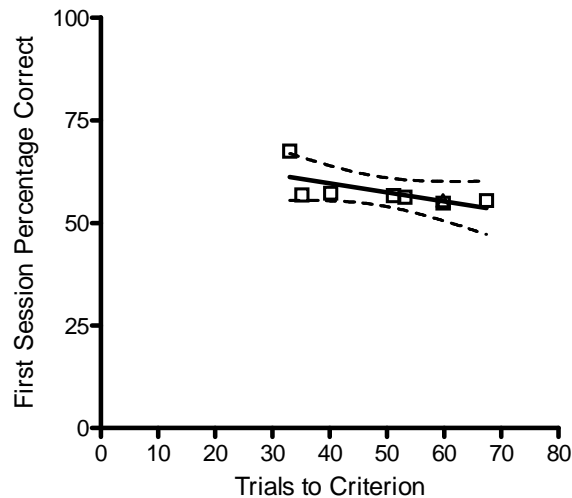


Figure 1. Bivariate regression of average number of trials to reach criterion on training task plotted against average percent correct on first session of testing once criterion was reached, for each individual subject.

In examining the number of trials to reach criterion across all training tasks, the average number of trials required varied according to task, and also varied by individual, (Megan’s average = 33, Mindy’s average = 67, SEM: 4.89). There was more variance in the performance of the individuals who required a greater number of trials to reach criterion overall, as can be seen in Figure 2, which shows the average number of trials to reach criterion across all training tasks. However, the individual differences in acquisition were not significant when subjected to an ANOVA of trials to criterion (including tasks of all types) with subject as factor, $F(6, 651) = 0.65, p = 0.69$. This result did not differ if the analysis included data for only those experiments in which all seven subjects participated, $F(6, 563) = 0.75, p = 0.61, \eta^2 = 0.008$.

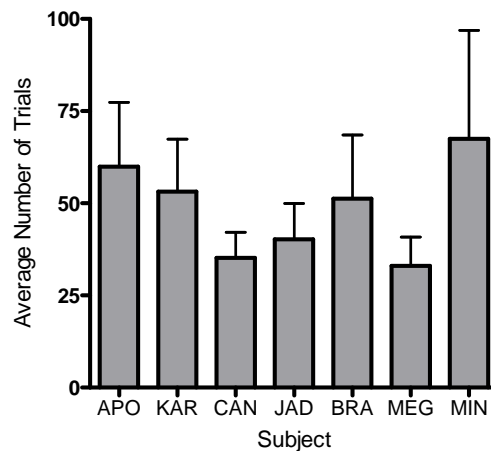


Figure 2. Average number of trials to reach criterion on all training tasks for each subject.

Although Megan, who required the fewest sessions to reach criterion, and therefore was the fastest learner, did not differ significantly in her acquisition rate from the slowest learners (Mindy and Apollo), when we examined performance on the first trial of testing, Megan’s performance did differ significantly from that of Apollo (Tukey HSD = 12.61, $p = 0.03$), and Mindy (Tukey HSD = 12.00, $p = 0.05$), and approached a significant difference from that of Kara (Tukey HSD = 11.21, $p = 0.08$) in an ANOVA of subject and first session performance on all testing sessions, $F(6, 695) = 2.33, p = 0.03$ (see Fig. 3). This result still obtains if only the experiments which all subjects participated in are included in the analysis, $F(6, 575) = 2.18, p = 0.04, \eta^2 = 0.02$. However, in this analysis, Megan and Mindy are the only two whose first session performance significantly differs from each other according to Tukey HSD comparisons (Megan: 69.15, $p = 0.05$, Mindy: 55.27, $p = 0.05$). Interestingly, this result indicates some consistency in performance differences across two different measures of performance (first session performance – mastery and trials to criterion – acquisition).

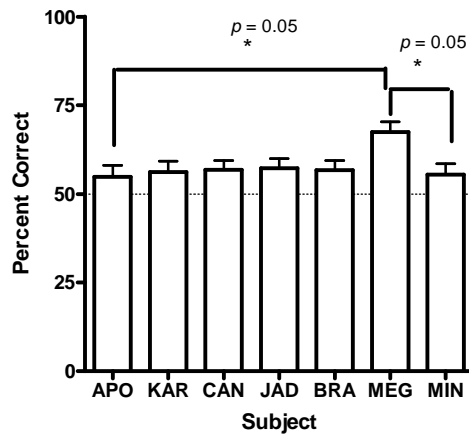


Figure 3. Average percent correct on first session of testing across all tests for each subject.

Individual Differences

Consistent with the significant relationship between two measures of performance (acquisition and mastery) as shown by the HLM analysis, the results of our tests so far indicate limited evidence for consistency across subjects in terms of best and worst performers. Therefore, we next asked whether there was consistency in performance within individuals across types of tasks in terms of the cognitive domain (social versus physical) and in terms of whether the task was measuring initial mastery or retention (old versus novel tasks). Here we used the same measures of performance analyzed previously – trials required to reach criterion, and first testing session performance.

Social versus Physical Tasks. We first performed an ANOVA on overall trials to criterion with type of task (social versus physical) and subject as factors and found no significant effects, p 's > 0.05. However, when we included only the data from experiments that all seven subjects participated in, there was a main effect of task with subjects generally requiring more trials to reach criterion on the social tasks, $F(1, 571) = 12.03, p = 0.001, \eta^2 = 0.02$. A glance at Figure 4 reveals that the difference is most pronounced for Jadine and does not appear to be significant for Kara, although the analysis did not reveal subject effects, or an interaction.

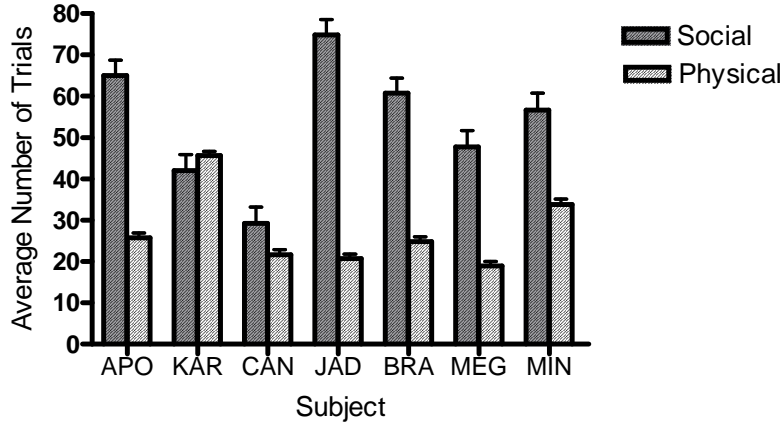


Figure 4. Average number of trials to reach criterion on training tasks for each subject, depending on whether task was classified as tapping into social or physical knowledge.

This difference does not appear to hold up for Jadine when assessing first session performance; however Brandy and Apollo’s first session performances appear to differ significantly between social and physical tasks (see Fig. 5). An ANOVA comparing subjects’ first session testing performance on social versus physical tasks revealed significant effects of both subject, $F(6, 688) = 2.31, p = 0.03$, and task type (social versus physical), $F(1, 688) = 20.94, p < 0.001$. Including only the data for which all subjects participated reveals the same effects of subject, $F(6, 568) = 2.37, p = 0.03, \eta^2 = 0.02$, and task type, $F(1, 568) = 25.06, p < 0.001, \eta^2 = 0.04$. Generally, subjects performed better on the first session of social rather than physical tasks. Recall that an overall analysis of first session performance revealed that Megan significantly outperformed Apollo and tended to outperform Mindy.

In order to gain additional information, we conducted two separate ANOVAs on testing data; one for social tasks only, and one for physical tasks only, to determine if there were any significant differences between subjects’ performances when we did this, despite the lack of significance between subject and task type in the overall interaction. On social tasks at testing, first session performance approached a significant difference only for Mindy and Megan (Tukey HSD = 15.48, $p = 0.06$). On physical tasks at testing, performance approached a significant difference only between Megan and Apollo (Tukey HSD = 15.71, $p = 0.09$) and Megan and Brandy (Tukey HSD = 16.32, $p = 0.07$). One interesting result from Figures 6A and 6B is that Megan performs accurately on the first sessions of both social and physical tasks; however, Brandy and Apollo who do fairly well at social tasks perform relatively poorly, compared to their peers, on physical tasks. Thus, while the results may reveal evidence for both consistency, or domain-general intelligence, a more plausible interpretation may be that there is domain specificity in cognitive skills that vary by individuals, and some individuals excel in both domains.

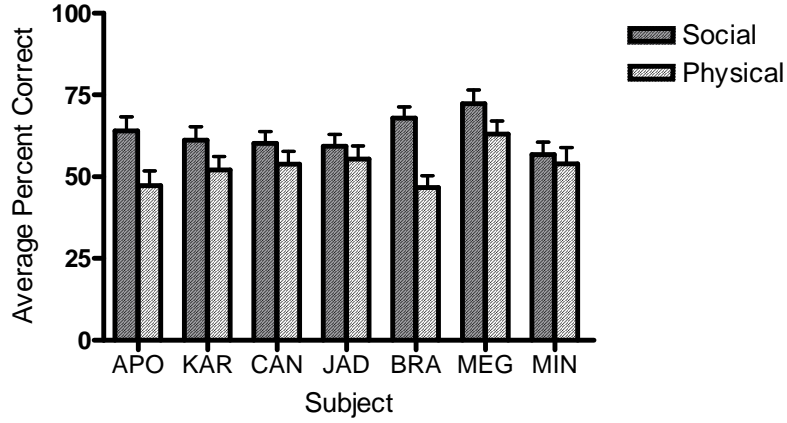


Figure 5. Average percent correct on first session of testing for each subject, depending on whether task was classified as tapping into social or physical knowledge.

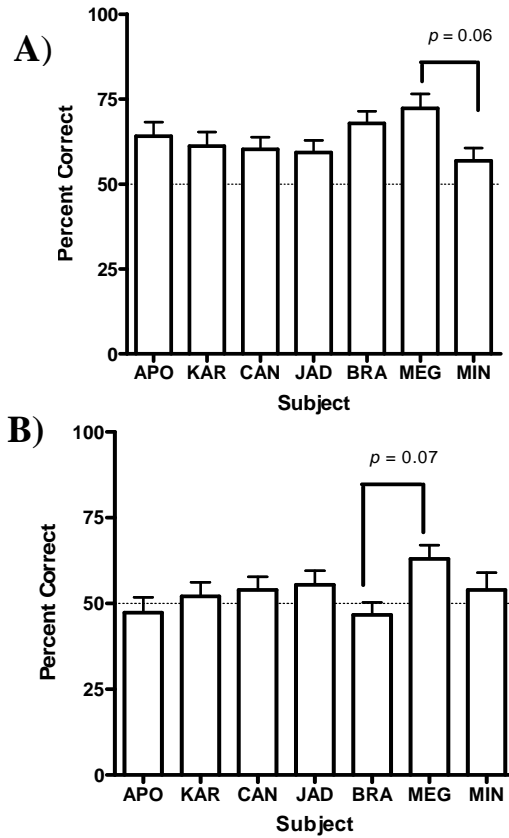


Figure 6. **A)** Average percent correct on first session of testing of social tasks showing an almost significant difference between Megan and Mindy's performance. **B)** Average percent correct on first session of testing of physical tasks showing an almost significant difference between Megan and Brandy's performance.

Novel versus Familiar/Retention and Transfer Tasks. Finally, we assessed whether individuals who excelled at novel tasks also excelled at generalizing that knowledge on transfer tasks, and were better able to retain that knowledge over time. To this end, we performed an ANOVA on trials to criterion, including both social and physical tasks, with type of task (novel, familiar and transfer) and subject as factors, and found a significant effect of task type, $F(2, 657) = 7.49, p < 0.001$. Not surprisingly, subjects required more trials to master novel tasks compared to familiar (Tukey HSD = 50.86, $p = 0.002$) and transfer tasks (Tukey HSD = 50.77, p 's = 0.002). Again, this effect still obtained if only data on which all subjects participated was included in the analysis, $F(2, 564) = 5.73, p = 0.003, \eta^2 = 0.02$. Figure 7C reveals that subjects are fairly homogenous on trials to reach criterion on transfer tasks; however Megan still requires the fewest trials to reach criterion while Mindy still requires the most. Candy, however, modestly outperforms Megan in learning novel tasks, and Jadine outperforms both in retention tasks (see Fig 7A). Retention tasks may reveal the use of memory rather than a purer measure of intelligence or skill per se.

Recall that Megan generally outperformed her peers, especially Apollo and Mindy in terms of first session performance overall. If we divide the tasks in terms of whether they are novel, generalization, or retention tasks, evidence for Megan's superiority remains. Again, we conducted an overall ANOVA on first session performance on testing data only with task type (novel, familiar and transfer) and subject as factors, and again there was a significant effect of task, $F(2, 681) = 18.26, p < 0.001$, and subject, $F(6, 681) = 3.00, p < 0.01$. The effects are the same including only data on which all subjects participated; subject effect, $F(6, 561) = 2.64, p = 0.02, \eta^2 = 0.03$, task effect, $F(2, 561) = 17.18, p < 0.001, \eta^2 = 0.06$. First session performance was significantly better on retention tasks than on novel (Tukey HSD = 9.99, $p = < 0.001$) or transfer tasks, (Tukey HSD = 14.68, $p < 0.001$), as can be seen in Figure 8. When ANOVAs were separately conducted for each task type, and Tukey post hoc tests were conducted to determine subject differences, for retention tests, Megan's first session performance approached a significant difference from Candy's (Tukey HSD = 19.77, $p = 0.07$) and Mindy's (Tukey HSD = 18.16, $p = 0.08$). For novel tasks, Megan's first session performance approached a significant difference only from Brandy's (Tukey HSD = 26.57, $p = 0.06$) and Jadine's (Tukey HSD = 25.91, $p = 0.08$). For generalization tasks, there was no significant effect of subject (see Fig. 8).

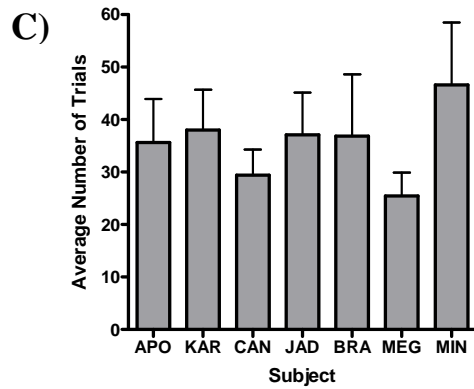
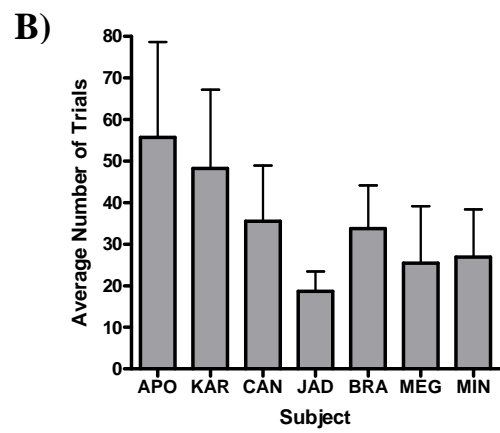
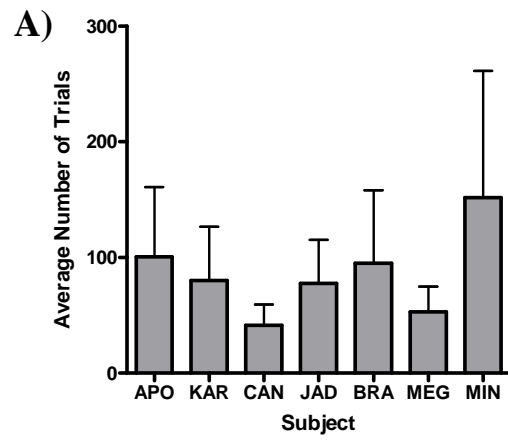


Figure 7. Average number of trials to reach criterion on retention for **A)** familiar tasks, **B)** novel tasks, and **C)** transfer or generalization tasks by subject.

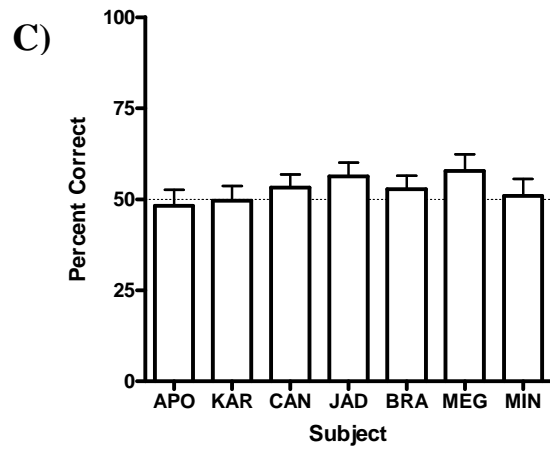
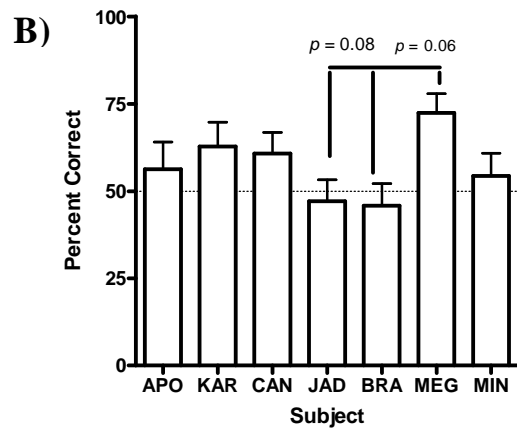
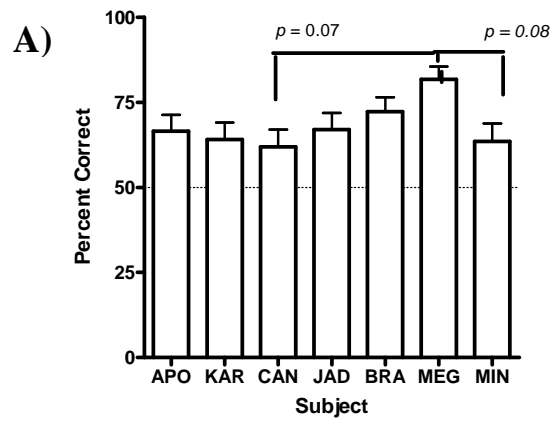


Figure 8. Average percent correct on **A)** retention or familiar tasks, **B)** novel tasks, and **C)** transfer or generalization tasks by subject.

Discussion

The one finding that stands out from the multiple comparisons is that Megan consistently outperforms her peers, albeit marginally, on measures of both acquisition and mastery, and on tests of both social and physical aspects of her environment. Whereas Megan performed equally well on both social and physical tasks, others showed more specialized “intelligence” in these domains. Apollo and Brandy performed better on first session performance in social (vs. physical) tasks, although this did not include trials to reach criterion in training for these tests. However, one could plausibly argue that first session performance is a more valid measure of social versus physical reasoning than the training tests established to familiarize them with the testing procedure. If true, individual differences might be more likely to be revealed during first session performance rather than in measures of acquisition (trials to reach criterion). So, although the same individual who excelled overall also excelled in both tests of social and physical reasoning, some individuals showed clear differences in their abilities to reason in these different types of tasks.

These results tentatively suggest that there is a significant amount of individual variation in cognitive ability in chimpanzees, as there is in humans. As with humans, one might expect to find individuals who display some general intelligence who will excel compared to their peers on a variety of cognitive tests (consistent with the ideas of Deaner et al., 2006; Lee, 2007). Others will find many tests difficult. Still others will show specialized skills and will excel in some domains more than in others. While we did not obtain strong evidence for a correlation between acquisition, mastery and generalization of knowledge, we did show that the same individuals who performed well in these measures did so consistently, and the same individuals who performed more poorly, also did so consistently. More interestingly, we showed some separation of ability within social and physical domains, and variability within those types of tasks, even within our small sample size.

Herrmann et al. (2010) tested a much larger group of chimpanzees, as well as human children, and determined no separate dimensions of social and physical cognitive intelligence in accounting for individual cognitive variability in chimpanzees. Obviously our smaller sample and fairly small effects cannot strongly challenge such conclusions, and our respective approaches and analyses were quite different. However, we tested our chimpanzees over a significant period of their lives and presented them with a much larger number of tasks (over 135 tasks over a decade versus 15 tasks in a period of days, Herrmann et al., 2007). Herrmann et al. (2007, 2010) also concluded that humans may differentiate themselves from other apes in the social domain, and may be more similar to other apes in the physical domain. In contrast, we are inclined to agree with a sentiment briefly alluded to by Herrmann et al. (2007) that where humans stand apart from their closest living relatives is in their ability to reason about unobservable causal forces, only one dimension of which may be mental states (Vonk & Povinelli, 2006). Also notably, the children were required to reason about members of their own species, whereas the apes were required to reason about members of another species in the Herrmann et al. study, potentially explaining some of the differences

in performance between children and apes on the social tasks. With the current project, we focused instead on whether individual chimpanzees differed in how they performed social versus physical tasks and found some evidence that they did. Lyn et al. (2010) have also raised concerns with Herrmann et al.'s (2007) conclusion regarding differences between apes and children on social tasks, because, in their own semi-replication with enculturated and non-enculturated apes, they found that apes who were reared in environments more similar to that of human children, did not differ significantly from children in measures of at least communicative skill. They suggest that rearing environment needs to be considered along with species differences – an important point to consider when testing small numbers of subjects, and another impetus for this project concerning individual differences. Both rearing environment and testing history will figure significantly in an animal's performance beyond any contributions of genetic endowment.

Much recent empirical work has been focused on the question of whether chimpanzees have a theory of mind (Povinelli & Vonk, 2003; Tomasello et al., 2003a, b; Vonk & Povinelli, 2006). The current corpus of data has been mounting in favor of granting chimpanzees (and many other species) the ability to attribute some mental states (such as seeing) to other beings. If one finds this data and the current popular interpretation convincing (although see Penn & Povinelli, 2007; Povinelli & Vonk, 2003, 2004; Vonk & Povinelli, 2006), one might expect chimpanzees to excel at problems of a social nature – those requiring them to reason about the minds of other beings. However, chimpanzees are also astute problem solvers when it comes to gathering food, using tools, finding shelter and dealing with other aspects of their physical environment. So regardless of whether they can reason about the thoughts and emotions of others, it is not a fait accompli that they should be more amendable to solving such problems than those of the physical nature. Parallels are sometimes drawn between the mental lives of chimpanzees and individuals with autism as both populations have been described as lacking or being deficient in theory of mind. Children with autism sometimes excel at tasks analogous to theory of mind problems, but designed to remove the mental component (Zaitchick, 1990). We would suggest that more empirical work be directed at such questions. Rather than focusing merely on what attributes our closest living relatives may share with us, it is equally fascinating to determine ways in which their minds may differ from ours, and the manner in which evolution may have selected for different cognitive priorities in different, but similar species.

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Appendix

A list of all experiments by project code, task (training or testing), type (new= acquisition, old=retention, tran=transfer or generalization or novel task), category (social or physical) with a brief description and a list of all participants who completed the experiment.

Experiment	Task	Type	Category	Description	Participants
96vsr1	Training	Old	Social	required action	APO, KAR, CAN, JAD, BRA
96vsr1	Training	Old	Social	required action	APO, KAR, CAN, JAD, BRA
95pnt0	Training	Tran	Social	discriminating, cue attending, object choice	CAN
95pnt0	Testing	Tran	Social	discriminating, cue attending, object choice	CAN
95pnt1	Training	New	Social	cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
95pnt1	Training	Tran	Social	cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
95pnt1	Testing	Tran	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
95pnt2	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
95pnt2	Testing	Tran	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
95pnt3	Training	Tran	Social	discriminating, object choice, cue attending	APO, KAR, CAN, JAD, BRA, MEG, MIN
95pnt3	Testing	Tran	Social	discrimination, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-1 1	Training	New	Social	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-1 1	Testing	New	Social	causal, intentional	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-1 2	Training	New	Social	causal, required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-1 2	Testing	Tran	Social	causal	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 1	Training	New	Social	causal	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 1	Training	New	Social	causal	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 1	Training	Old	Social	causal, cue attending	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 1	Testing	New	Social	causal, perspective-taking	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 1	Testing	New	Social	causal, perspective-taking	APO, KAR, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
93-Int-2 1	Testing	New	Social	causal, perspective-taking	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 1	Testing	New	Social	causal, perspective-taking	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 1	Testing	New	Social	causal, perspective-taking	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 1	Testing	New	Social	causal, perspective-taking	APO, KAR, JAD, BRA, MEG, MIN
93-Int-2 7	Training	Old	Social	causal, perspective-taking	APO, KAR
93-Int-2 11	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 11	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 18	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 19	Testing	Tran	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-219	Testing	Tran	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
93-Int-2 19	Testing	Tran	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 20	Testing	Tran	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 21	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 21	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 21	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 21	Testing	Tran	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 22	Testing	Tran	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
93-Int-2 22	Testing	Old	Social	causal, perspective-taking	APO, KAR, CAN, JAD, BRA, MEG, MIN
92-GK 1	Testing	New	Social	causal, knowledge states	APO, KAR, BRA, MEG, MIN
92-GK 2	Testing	Tran	Social	causal, knowledge states	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-ATN	Testing	New	Social	discriminating, intentionality	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 8	Testing	Old	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 9	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 9	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 9	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 9	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 9	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 9	Testing	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA10	Testing	Tran	Social	discriminating, object choice	JAD, BRA
94-JVA 11	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
94-JVA 11	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 11	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 11	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 11	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 12	Training	Tran	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 12	Testing	Tran	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 13	Training	Tran	Social	discriminating, cue attending	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 13	Testing	Tran	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 14	Training	New	Social	discriminating, food competition	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 14	Training	New	Social	discriminating, cue attending, food competition	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 14	Testing	Tran	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 15	Training	Old	Social	discriminating, cue attending	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 15	Testing	Old	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 16	Training	Old	Social	discriminating, cue attending, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 16	Testing	Old	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 18	Training	Tran	Social	discriminating, object choice, cue attending	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 18	Training	Tran	Social	discriminating, object choice	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-JVA 18	Testing	Tran	Social	discriminating, object choice, cue attending	APO, KAR, CAN, BRA, MEG
94-JVA 18	Testing	Tran	Social	discriminating, object choice	APO, KAR, CAN, BRA, MEG
96- VSR1	Training	Old	Social	causal, visual perspective-taking	KAR, CAN, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
96- VSR1	Training	Old	Phys	required action	KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE1	Testing	New	Phys	explanatory drive	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE2	Training	New	Phys	explanatory drive, motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE2	Testing	New	Phys	explanatory drive	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE3	Training	New	Phys	explanatory drive, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE3	Testing	New	Phys	explanatory drive,	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE4	Training	New	Phys	explanatory drive, motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE4	Testing	Tran	Phys	explanatory drive,	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE5	Training	New	Phys	explanatory drive, required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE6	Training	New	Phys	explanatory drive, required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE6	Testing	Tran	Phys	explanatory drive	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE8	Training	Old	Phys	explanatory drive, motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE8	Testing	Tran	Phys	explanatory drive	APO, KAR, CAN, JAD, BRA, MEG, MIN
97-CAUSE9	Training	New	Phys	explanatory drive, discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS0	Training	New	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS1	Testing	Trans	Phys	discrimination, weight	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS2	Testing	Trans	Phys	discrimination, weight	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS3	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS3	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS3	Testing	Tran	Phys	discrimination, weight	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS4	Training	Tran	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS4	Training	Tran	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS4	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS5	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG

Experiment	Task	Type	Category	Description	Participants
99-PHYS5	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS5	Testing	New	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS6	Training	Old	Phys	causal, motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS6	Training	Old	Phys	causal, motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS6	Testing	New	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS7	Training	Tran	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS7	Testing	Tran	Phys	discrimination, weight	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS8	Testing	Tran	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS9	Testing	Old	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MIN, MEG
99-PHYS10	Testing	Tran	Phys	causal, functional weight	APO, CAN, JAD, BRA, MEG
99-PHYS11	Training	New	Phys	causal, motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS11	Training	Old	Phys	causal, discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS11	Testing	New	Phys	causal, balance	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS12	Testing	Tran	Phys	causal, balance	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS13	Training	New	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS13	Testing	New	Phys	causal, balance	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS14	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS14	Testing	Old	Phys	causal, balance	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS15	Training	Tran	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS15	Testing	New	Phys	causal, rigidity	APO, KAR, CAN, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
99-PHYS16	Training	Tran	Phys	causal, discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS16	Testing	Tran	Phys	causal, rigidity	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS19	Training	Old	Phys	causal, discrimination	KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS19	Testing	New	Phys	causal, rigidity	KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS17	Testing	Tran	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS17	Testing	Tran	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS17	Training	Old	Phys	causal, required action	APO, KAR, CAN, JAD, BRA, MIN, MEG
99-PHYS17	Training	Old	Phys	causal, required action	APO, KAR, CAN, JAD, BRA, MIN, MEG
99-PHYS17	Training	New	Phys	causal, required action	APO, KAR, CAN, BRA, MEG, MIN
99-PHYS17	Training	Old	Phys	causal, required action	APO, KAR, CAN, BRA, MEG, MIN
99-PHYS 17	Testing	Trans	Phys	causal	JAD
99-PHYS18	Testing	Old	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MIN, MEG
99-PHYS18	Testing	Old	Phys	causal	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS20	Training	Old	Phys	discrimination, required action	APO, KAR, CAN, JAD, BRA, MIN, MEG
99-PHYS20	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS20	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS20	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS20	Testing	Tran	Phys	discrimination, weight	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS22	Training	Old	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS22	Training	New	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS22	Training	Old	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
99-PHYS22	Training	Old	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG
99-PHYS22	Testing	Tran	Phys	causal, functional weight	APO, KAR, CAN, JAD, BRA, MEG

Experiment	Task	Type	Category	Description	Participants
02-PSB1	Training	Tran	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PSB1	Training	New	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PSB1	Training	Tran	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PSB1	Training	Tran	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PSB2	Training	Tran	Phys	tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PMP1	Training	New	Phys	motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PMP1	Training	Tran	Phys	motor action	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PMP2	Training	New	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
02-PMP3	Training	Old	Phys	tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-ATN	Training	Old	Phys	motor action	APO, KAR, JAD, BRA, MEG, MIN
94-ATN	Training	New	Phys	discrimination	APO, KAR, JAD, BRA, MEG, MIN
94-ATN	Training	Tran	Phys	discrimination	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL1	Training	New	Phys	causal, tool competence	KAR, JAD, BRA, MEG
94-TOOL1	Training	Old	Phys	causal, tool competence	KAR, JAD, BRA, MEG
94-TOOL1	Testing	Tran	Phys	causal, gravity	KAR, JAD, BRA, MEG
94-TOOL2	Training	New	Phys	tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL2	Testing	New	Phys	causal, gravity	APO, KAR, JAD, BRA, MEG, MIN
94-TOOL3	Training	Old	Phys	tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL3	Testing	Tran	Phys	causal, gravity	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL4	Training	Tran	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL4	Testing	New	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL5	Testing	Old	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
94-TOOL6	Testing	Tran	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL7	Testing	New	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL7	Training	New	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL7	Testing	New	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL8	Training	New	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL8	Training	Tran	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL8	Testing	Tran	Phys	causal, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL9	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL9	Testing	New	Phys	causal, rigidity	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL10	Testing	Tran	Phys	causal, rigidity	JAD
94-TOOL11	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL11	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL11	Testing	Tran	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL11	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MIN
94-TOOL11	Testing	Tran	Phys	causal, connection	CAN, BRA, MEG
94-TOOL12	Training	New	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL12	Training	New	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL12	Testing	Tran	Phys	causal, tool competence, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL13	Training	Tran	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL13	Testing	Tran	Phys	causal, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
94-TOOL14	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL14	Testing	Old	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL15	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL15	Testing	Old	Phys	causal, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL16	Training	Tran	Phys	causal, tool competence	APO, KAR, JAD, BRA, MEG, MIN
94-TOOL16	Testing	New	Phys	causal, tool competence, shape	APO, KAR, JAD, BRA, MEG, MIN
94-TOOL17	Testing	Tran	Phys	causal, tool competence, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL18	Testing	Tran	Phys	causal, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL19	Training	New	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL19	Training	Old	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL19	Testing	Tran	Phys	causal, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL19	Testing	Tran	Phys	causal, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL20	Training	Tran	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL20	Testing	Tran	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL21	Testing	Tran	Phys	causal, shape	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL22	Training	Tran	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL22	Testing	Tran	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL23	Training	Tran	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL23	Testing	Tran	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL25	Testing	New	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN

Experiment	Task	Type	Category	Description	Participants
94-TOOL26	Testing	Tran	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL27	Testing	Tran	Phys	causal, connection	APO, KAR, CAN, JAD, BRA, MEG, MIN
94-TOOL0	Testing	Tran	Phys	causal	MEG
94-TOOL28	Training	New	Phys	causal, tool competence	APO, KAR, CAN, JAD, BRA, MEG, MIN
03-PRC1	Training	Tran	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
03-PRC1	Training	Old	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
03-PRC2	Training	Old	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
03-PRC3	Training	Old	Phys	required action	APO, KAR, CAN, JAD, BRA, MEG, MIN
00-VIS0	Training	New	Soc	causal, food competition	KAR, CAN, JAD, BRA, MEG, MIN
00-VIS3	Testing	Tran	Soc	causal, food competition	KAR, CAN, JAD, BRA, MEG, MIN
00-VIS4	Testing	Tran	Soc	causal, food competition	KAR, CAN, JAD, BRA, MEG, MIN
00-VIS5	Testing	Tran	Soc	causal, food competition	KAR, CAN, JAD, BRA, MEG, MIN
00-VIS6	Testing	Tran	Soc	causal, food competition	KAR, CAN, JAD, BRA, MEG, MIN
00-VIS7	Testing	Tran	Soc	causal, food competition	KAR, CAN, JAD, BRA, MEG, MIN